

RODENTS AND LAGOMORPHS (MAMMALIA) FROM THE
LATE CLARENDONIAN (MIOCENE) ASH HOLLOW FORMATION,
BROWN COUNTY, NEBRASKAWILLIAM W. KORTH¹

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ABSTRACT

Twenty-five species of rodents and lagomorphs are recognized from Pratt Quarry, Brown County, Nebraska. Of these, four are new: the beaver *Dipoides tanneri*, the heteromyid *Cupidinimus prattensis*, the cricetid *Antecalomys phthanus* (also new genus), and the leporid *Pronotolagus whitei*.

The rodent and lagomorph fauna from Pratt Quarry is clearly transitional between Clarendonian and Hemphillian because it contains the first record of four typically Hemphillian taxa (*Dipoides*, sigmodontine cricetids, *Hypolagus vetus*, leporine leporids), and the last record of eight Clarendonian or earlier taxa (*Protospermophilus*, *Petauristodon*, *Eucastor*, *Phelosacomys*, *Mioheteromys*, *Copemys*, *Tregomys*, and *Hesperolagomys*). This combination of first and last occurrences verifies a latest Clarendonian age for the fauna and the Merritt Dam Member of the Ash Hollow Formation.

KEY WORDS: Clarendonian, rodent, lagomorph, systematics

INTRODUCTION

Pratt Quarry was discovered in the 1930s and fossils were collected intermittently over the next 40 years by parties from the Frick Laboratory of the American Museum of Natural History (Skinner and Johnson, 1984). During these expeditions, 179 fossil mammal specimens were recovered, predominantly of larger mammals. The only rodents recovered were the larger beavers and some mylagaulid material. Screening for small vertebrates at Pratt Quarry was undertaken first in 1989 by a field party from the University of Nebraska State Museum. Again, in 1994, collection of microvertebrates was undertaken by the Rochester Institute of Vertebrate Paleontology, sponsored by the University of Nebraska. The screening operations have yielded several hundred identifiable specimens of small mammals which are the basis of this study. Previously, only the moles (Talpidae) from Pratt Quarry had been studied (Rudnick, 1992).

Pratt Quarry is in the Merritt Dam member of the Ash Hollow Formation (Skinner and Johnson, 1984). The age of the Merritt Dam Member has been established as late Clarendonian based on preliminary faunal analysis (Voorhies, 1990a). The legal location and a stratigraphic section of the quarry were presented by Skinner and Johnson (1984:310, fig. 26, 37). The quarry is a stream channel deposit that cuts into the underlying strata of the Cap Rock member of the Ash Hollow Formation and the Burge and Devil's Gulch members of the Valentine Formation.

There are four fossiliferous horizons at Pratt Quarry: 1) the base of the channel cut, 2) approximately 5 m above the base of the channel, 3) approximately 10 m above the channel base, and 4) a thin layer of diatomite at the top of the section approximately 20 m above the base of the channel. The fossils from the 5- and

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10-m horizons came from lenses of clay-ball conglomerates discontinuously exposed across the section. Among the clasts in the basal conglomerate are numerous bone fragments that are much more heavily worn than the majority of the fossils and appear to be reworked from the underlying strata. This difference in wear suggests that some of the faunal elements from the quarry may be reworked from these older layers. However, nearly all species identified here are from all levels. The only difference in occurrence of species throughout the section appears to be controlled by the dynamics of the depositing stream. The larger rodents (beavers, mylagaulids) are predominantly from the base of the section and are more poorly represented in the higher levels, whereas the smaller rodents (cricetids, heteromyids, sciurids) are most common from the horizon 10 m above the base of the channel. There is no definite proof that suggests any of the species of rodents or lagomorphs cited below are from horizons lower than the Merritt Dam member.

The rodents and lagomorphs from Pratt Quarry are significant because of the paucity of micromammals from the Clarendonian of the Great Plains. The only other micromammalian faunas of Clarendonian age from the Plains are the Mission fauna from South Dakota (Green, 1971) and the WaKeeney Fauna from Kansas (Wilson, 1968). Both of these latter faunas cannot be placed with confidence within the Clarendonian as early or later, and the Mission fauna of micromammals consists of fewer than 20 specimens of isolated teeth. The lithostratigraphic sequence that includes Pratt Quarry is well exposed and its relation to other layers in the local stratigraphic section is clearly defined. This relationship allows for a direct comparison of the fossils from Pratt Quarry to those from the subjacent strata and enhances the biostratigraphic value of the fauna.

Dental terminology used below for rodents follows that of Wood and Wilson (1936) with specialized terminology for castorids as defined by Stirton (1935). Lagomorph dental terminology used is that of White (1987, 1991). Abbreviations for institutions: AMNH, American Museum of Natural History; FAM, Frick Collections, AMNH; KU, University of Kansas Museum of Natural History; UNSM, University of Nebraska State Museum; UOMNH, University of Oregon Museum of Natural History; USNM, National Museum of Natural History, Smithsonian Institution. Abbreviations for dental measurements and statistical values are given in Table 1. Measurements in tables are given in millimeters.

SYSTEMATIC PALEONTOLOGY

Order Rodentia Bowdich, 1821

Family Mylagaulidae Cope, 1881

Mylagaulus Cope, 1881

Mylagaulus monodon Cope, 1881

(Fig. 1, Table 1)

Referred Specimens.—UNSM 101710–101717, isolated P₄; UNSM 101735, dP⁴; UNSM 101718–101724, 101796, isolated P⁴; UNSM 101729, fragmentary mandible with portion of lower incisor; UNSM 101725, proximal end of ulna; UNSM 101726, humerus; UNSM 101727, 101728, femora; UNSM 101732, ungual phalanx; UNSM 101797, astragalus; UNSM 101733, 101734, isolated incisors; UNSM 101736–101742, isolated molars.

Description.—The maximum length and width of both the upper and lower premolars are approximately at the level of the center of the tooth viewed laterally (half the maximum height of the tooth). In occlusal outline both premolars are elongated ovals. The occlusal pattern changes from fewer fossettes (-ids) in unworn specimens, to a greater number in moderately worn specimens. Upper

Table 1.—Dental measurements of premolars of *Mylagaulus monodon* from Pratt Quarry. Abbreviations of dental dimensions used in all later tables: a-p, anteroposterior length; tr, maximum transverse width; tra, anterior transverse width (protoloph of upper cheek teeth, metalophid of lower cheek teeth); trp, posterior transverse width (metaloph of upper cheek teeth, hypolophid of lower cheek teeth). Statistical abbreviations: n, number of specimens; M, mean; OR, range of size; s, standard deviation; CV, coefficient of variation. Crown height measured only on unworn or little worn specimens. Measurements in mm.

		n	M	OR	s	CV
P ₄	occlusal a-p	8	10.03	8.10–12.30	1.70	16.9
	occlusal tr	8	5.24	4.45–6.85	0.72	13.7
	maximum a-p	8	11.04	9.80–12.30	1.02	9.2
	maximum tr	8	5.38	4.80–6.85	0.63	11.8
	crown height	5	15.94	14.60–17.80	1.33	8.3
P ⁴	occlusal a-p	6	8.72	7.20–10.95	1.46	16.7
	occlusal tr	6	5.62	4.45–6.40	0.70	12.4
	maximum a-p	6	9.56	8.15–10.95	1.01	10.6
	maximum tr	6	5.82	4.90–6.40	0.59	10.1
	crown height	3	13.53	11.30–16.30	2.54	18.8

premolars are concave on the lingual side for their entire height, whereas lower premolars are essentially straight-sided throughout their entire crown height.

In moderate wear, upper premolars have eight fossettes. All fossettes are narrow and anteroposteriorly oriented. There are three fossettes along the posterior margin (one lingual, one central, one buccal). A small fossette is near the center of the buccal margin of the tooth. Anteriorly there are three major fossettes arranged similarly to the posterior fossettes, and an additional, smaller fossette near the center of the anterior margin of the tooth. In earlier stages of wear, these eight fossettes are commonly fused to one another forming "star-like" fossettes. On an unerupted P⁴ (UNSM 101721), there are only four recognizable fossettes: the central posterior fossette is fused with the central buccal fossette, the anterior and posterior lingual fossettes are fused, and the small central anterior fossette is fused with the main central anterior fossette in a "forked" shape. In the specimens showing little wear the anterior central fossette is always forked and the other fossettes are randomly fused, eventually to be separated into seven fossettes in later wear. In the most heavily worn specimens the fossettes are all nearly straight and anteroposteriorly oriented. Each fossette is distinct and never fused with another.

On the buccal sides of the lower premolars is a shallow groove that runs the entire height of the tooth. In early stages of wear there are as few as six fossettids on the occlusal surface: three along the posterior margin of the tooth, a single reentrant valley from the lateral groove on the tooth, a central anterior fossettoid that is anteriorly forked, and a small fossettoid on the anterior half of the tooth along the lingual margin. Commonly, there is a minute, circular accessory fossettoid which occurs at different places on the tooth. In later stages of wear, the forked anterior fossettoid splits into two and the number of fossettids is seven or eight. Like the upper premolars, in the very late stages of wear all the fossettids are nearly straight anteroposteriorly and do not fuse with one another.

Discussion.—The specimens referred here to *Mylagaulus monodon* are intermediate in size between the Hemphillian *Mylagaulus* from Oregon (Wilson, 1937) and Barstovian species identified as *M. cf. laevis* (Gazin, 1932; Storer, 1975; Voorhies, 1990b). The number of fossettes (-ids) on the premolars is also greater than those from the Barstovian.

In size, crown height, and complexity of the occlusal surface of the premolars, the Pratt Quarry species is comparable to both the holotype of *M. monodon* (Cope and Matthew, 1915:pl. CXIXc, fig. 11) and the sample of *Epigaulus minor* from Kansas (Hibbard and Philis, 1945). In the original description of *E. minor*, Hibbard and Philis (1945) suggested that this species might be conspecific with *M. monodon*. The difference between the genera *Mylagaulus* and *Epigaulus* is the presence of horn cores on the nasal bones of the latter. Because the holotype of

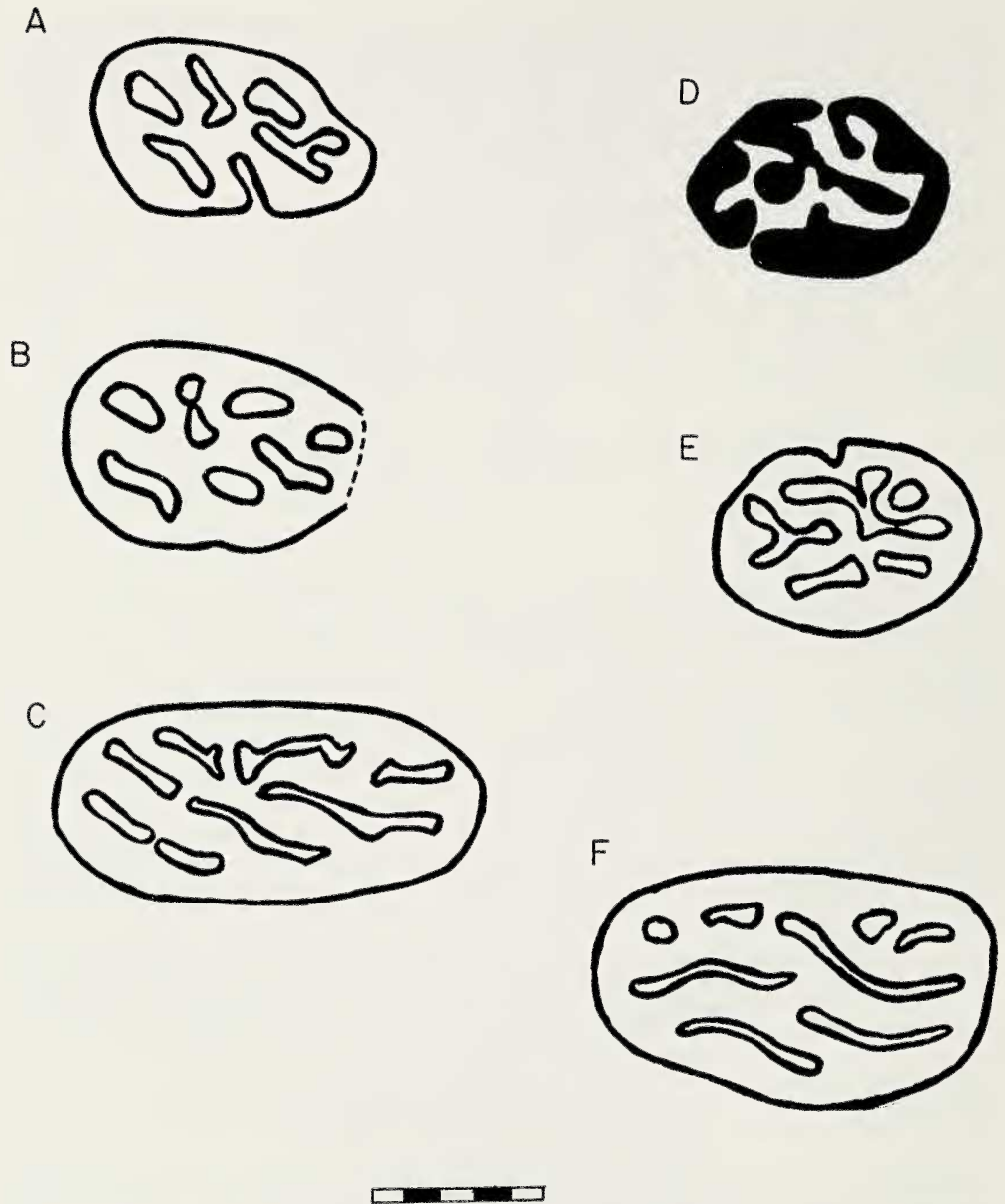


Fig. 1.—Premolars of *Mylagaulus monodon* from Pratt Quarry showing differing stages of wear: least worn (top) to late stages of wear (bottom). A–C, right P₄. A, UNSM 101713. B, UNSM 101714. C, UNSM 101715. D–F, left P₄. D, UNSM 101721 (unworn). E, UNSM 101718. F, 101723. Bar scale = 5 mm.

M. monodon does not include any skull material, the presence or absence of horn cores is unknown. If the holotype of *E. minor* were not a skull, this material might well have been referred to *Mylagaulus*. In fact, the type species of *Mylagaulus*, *M. sesquipedalis*, is known only from an isolated upper premolar. The presence or absence of horn cores is clearly not part of the definition of the genus.

Another difficulty with the synonymy of *M. monodon* and *E. minor* is the age of occurrence. *Epigaulus minor* is clearly from the Clarendonian WaKeeney fauna of Kansas. The holotype of *M. monodon* is most likely from the late Barstovian of southwestern Nebraska (Voorhies and Xue, 1983; Fiorillo, 1988; Voorhies, 1990a). Dentally, these species cannot be separated, therefore, the older name, *Mylogaulus monodon*, is used here.

The postcranials referred here to *M. monodon* are also identical in morphology and size to those of *E. minor* (Hibbard and Philis, 1945), and larger and more robust than those of the Barstovian *M. laevis* (Fagan, 1960).

Family Sciuridae Gray, 1821

Subfamily Sciurinae Gray, 1821

Tribe Marmotini Pocock, 1923

Protospermophilus Gazin, 1930

Protospermophilus sp., cf. *P. quatalensis* Gazin, 1930
(Fig. 2A)

Referred Specimen.—UNSM 101765, isolated M¹ or M².

Measurements.—a-p, 2.46 mm; tr, 2.72 mm.

Description and Discussion.—This specimen is separable from the remainder of the sciurines in the fauna by its greater relative length. In both species of *Spermophilus* and *Ammospermophilus* discussed below, the upper molars have a much greater transverse width than anteroposterior length. In UNSM 191765, the length is closer to the width, giving the tooth a much more squared appearance. There is a large cuspule at the lingual end of the posterior cingulum (= hypocone) characteristic of *P. quatalensis*. The only difference between UNSM 101765 and the M¹ of *P. quatalensis* from California (Black, 1963:pl. 13, fig. 4b) is the deep notch separating the protocone and hypocone which is lacking on the Pratt Quarry specimen. This notch on M¹ is a diagnostic character of *P. quatalensis*; however, the Nebraska specimen may well be an M². The M² of *P. quatalensis* does not have as pronounced a notch as the M¹.

Protospermophilus quatalensis has been reported only from the latest Barstovian and earliest Clarendonian of California (Gazin, 1930; Bryant, 1945). This occurrence of *Protospermophilus* extends the record of the genus to the late Clarendonian.

Spermophilus Cuvier, 1825

Spermophilus (*Otospermophilus*) Brandt, 1844

Spermophilus (*Otospermophilus*) sp.

(Fig. 2F–H, Table 2)

Referred Specimens.—UNSM 101590, 101799, isolated dP⁴; UNSM 101585–101589, 101591, 101746, 101765, isolated M¹ or M²; UNSM 101583, edentulous maxilla; UNSM 101580, 101584, 101766, 101767, isolated M₁ or M₂; UNSM 101578, 101581, isolated M₃; UNSM 101579, 101582, partial mandibles without cheek teeth.

Description.—The lower molars are brachydont and cusped, typical of the subgenus *Otospermophilus*. The lower premolar is not represented in the collection. The anterior molars are rhomboidal in occlusal outline, and wider than long. The first molar cannot be differentiated with certainty from M₂. The anterior width of the molars (metalophid) is less than the posterior half of the tooth. The metaconid, protoconid, and hypoconid are bulbous, showing little or no compression. The entoconid is reduced to a curve at the lingual end of the posterolophid. The lingual half of the tooth is shorter (anteroposteriorly) than the buccal half. There is a minute mesostylid present on all specimens. The trigonid basin is small and obliquely oriented, bounded anteriorly by a ridge running buccally from the apex of the metaconid (metalophid I), and bounded posteriorly by a short posterior arm of the protoconid. The trigonid basin is slightly open posteriorly because the posterior arm of the protoconid (metalophid II) is not continuous with the base of the metaconid. The ectolophid is weak, and on little-worn specimens a minute mesoconid is present.

The last lower molar is similar to M₁ and M₂ except it is elongated posteriorly and has a narrower posterior half. There is evidence of a small mesoconid and mesostylid on M₃.

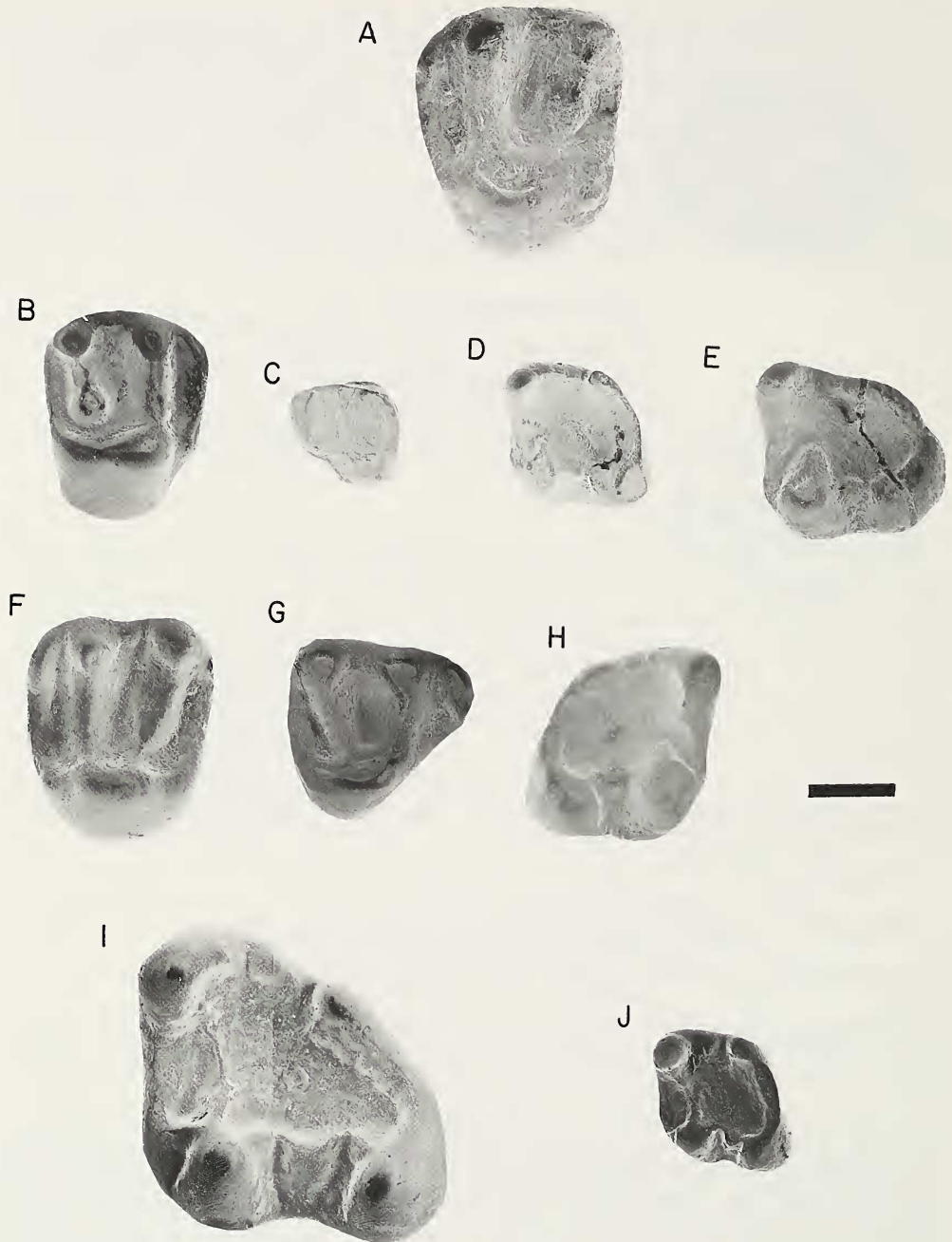


Fig. 2.—Scanning electron micrographs of cheek teeth of sciurids from Pratt Quarry. A, *Protospermophilus* sp., cf. *P. quatalensis*, left M¹ or M², UNSM 101765. B–E, *Ammospermophilus juturensis*. B, right M¹ or M², UNSM 101762. C, left P₄, UNSM 101755. D, left M₁ or M₂, UNSM 101758. E, left M₃, UNSM 101763. F–H, *Spermophilus (Otospermophilus)* sp. F, left M¹ or M², UNSM 101746. G, right dP⁴, UNSM 101590. H, right M₁ or M₂, UNSM 101766. I, ?*Petauristodon* sp., left M₃, UNSM 101659. J, cf. *Sciurion* sp., left M₁ or M₂, UNSM 101769. Bar scale = 1 mm.

Table 2.—Dental measurements of *Spermophilus* (*Otospermophilus*) sp. from Pratt Quarry. Abbreviations as in Table 1. Measurements in mm.

UNSM No.	M ₁ or M ₂			M ₃			P ₄ -M ₃	dP ⁴		M ¹ or M ²	
	a-p	tra	trp	a-p	tra	trp		a-p	tr	a-p	tr
101578				—	2.12	—					
101580	1.89	1.92	2.15								
101581				2.90	2.72	2.41					
101584	1.99	2.10	2.13								
101579							8.75				
101766	1.96	2.23	2.09								
101585										2.01	2.42
101586										2.21	2.89
101587										2.45	2.98
101588										2.25	2.96
101589										2.00	2.67
101590								2.04	1.99		
101591										2.00	—
101799								2.02	1.88		

The mandible is generally slender, but more heavily built than in species of the subgenus *Spermophilus*. The masseteric scar is U-shaped. It ends anteriorly below the posterior roots of P₄. The dorsal margin of the diastema is shallow. The mental foramen is high on the side of the mandible, just below the margin of the diastema, approximately at its center. The lower incisor is elongated anteroposteriorly in cross section and strongly convex anteriorly. Enamel covers approximately half of the tooth on its lateral side.

The single dP⁴ (UNSM 101590) is triangular in occlusal outline. There is a large parastyle (= anterocone) on the anterobuccal corner of the tooth continuous with the anterior cingulum. It is crescentic in shape, and defines a wide valley between the anterior cingulum and the protoloph. Both the protoloph and metaloph converge on the protocone and are continuous with it. There is no evidence of a protoconule, but there are two minute wear facets on the metaloph indicating a doubled metaconule. The posterior cingulum runs the entire width of the tooth and ultimately runs into the apex of the protocone. On the posterior slope of the protocone is a small wear facet that indicates the presence of a small hypocone.

The upper molars are typical of other species of the subgenus *Otospermophilus*, and do not have the high degree of lophodonty as in species of *Spermophilus* (*Spermophilus*). The protoloph is complete from the paracone to the protocone with no protoconule. The metaloph ends lingually before meeting the protocone. There is a small metaconule at the lingual end of the metaloph. The anterior and posterior cingula are continuous from the buccal margin of the teeth and run nearly the entire width of the tooth. The anterior cingulum runs up the anterior slope of the protocone. The posterior cingulum is slightly longer than the anterior, and has a distinct bend at its lingual end as it fuses with the protocone. There is no evidence of a hypocone on any of the specimens. A small mesostyle is always present.

Discussion.—The cheek teeth of *Spermophilus* (*Otospermophilus*) sp. are proportioned as in other species of *Spermophilus* (wider than long), but do not have the amount of anteroposterior compression or lophodonty as in species of *S.* (*Spermophilus*). The only other species of *Spermophilus* from the Clarendonian are *S.* (*O.*) *matthewi* and *S.* (*Spermophilus*) sp. (= *Citellus* [*Citellus*] sp., Black, 1963). *Spermophilus* (*O.*) *matthewi* is markedly larger than *S.* (*O.*) sp. with a much more heavily built mandible (Black, 1963:202, pl. 18, fig. 2). The unnamed species of *S.* (*Spermophilus*), although similar in size to *S.* (*O.*) sp., is clearly distinguishable because of the greater compression and lophodonty of the lower cheek teeth that is characteristic of species of its subgenus (Black, 1963:pl. 22, fig.4).

The only other species of *S.* (*Otospermophilus*) similar in size to *S.* (*O.*) sp. are *S.* (*O.*) *argonautus* and *S.* (*O.*) *gidleyi*, both from the Hemphillian. *Spermo-*

philus (*O.*) *gidleyi* is diagnosed as having distinct ectostylids and posteriorly closed trigonids on the lower molars, whereas these features are lacking in *S. (O.)* sp. *Spermophilus (O.) argonautus* lacks the mesostylid and mesoconid on the lower molars that characterize *S. (O.)* sp. (Stirton and Goeriz, 1942:fig. 7e).

Spermophilus (Otospermophilus) sp. is surprisingly primitive with the possession of a mesoconid on the lower molars and only weakly lophate cheek teeth. Only the Barstovian species *S. (O.) primitivus* and *S. (O.) jerae* retain a mesoconid on the lower molars (Bryant, 1945; Black, 1963; Sutton and Korth, 1995). These species differ from *S. (O.)* sp. in size (*S. primitivus* larger, *S. jerae* smaller) and having better developed entoconids on the lower molars.

Ammospermophilus Merriam, 1892

Ammospermophilus junturensis (Shotwell and Russell, 1963)

(Fig. 2B–E, Table 3)

Citellus junturensis Shotwell and Russell, 1963.

Ammospermophilus? sp. Black, 1963.

Referred Specimens.—UNSM 101751, P³; UNSM 101592, 101752–101754, M¹ or M²; UNSM 101755, 101756, P₄; UNSM 101759, partial mandible with M₁–M₂; UNSM 101757, 101758, 101760, 101761, M₁ or M₂; UNSM 101762–101764, M₃.

Discussion.—Both the upper and lower dentitions of *Ammospermophilus junturensis* have been fully described by Shotwell and Russell (1963:44–46) and Black (1963:225–226). The specimens referred to this species from Pratt Quarry do not differ in size or morphology from the previously described material from Oregon. Specimens of *A. junturensis* from Pratt Quarry are easily separable from *Spermophilus (Otospermophilus)* in their smaller size. In addition, the lower molars are relatively wider with a more weakly developed ectolophid, and the upper molars have a larger, more distinct metaconule.

The fossil material from Pratt Quarry referred to *Ammospermophilus junturensis* is comparable in size and morphology to the topotypic material from Oregon (Black, 1963:226, pl. 22, fig. 6; Shotwell and Russell, 1963:table 6, fig. 38, 39). It differs from the only other Tertiary species of the genus, *A. fossilis*, in its slightly larger size (James, 1963:table 13).

Other than size, the most distinctive difference between the Tertiary species of *Ammospermophilus* and the Recent species is the morphology of anterior cingulum on the upper molars. In the Tertiary species it is less prominent and originates at the protocone, but does not have the 90° bend at its origin as do the molars of the Recent species (James, 1963).

Shotwell and Russell (1963) originally referred this species to *Citellus* (= *Spermophilus*). However, Black's (1963:225) arguments for assigning it to *Ammospermophilus* (based on the morphology of the lower cheek teeth) appear valid. Also, the similarity to the other Tertiary species, *A. fossilis*, which is known from cranial material, verifies the inclusion of *A. junturensis* in the genus *Ammospermophilus*.

Subfamily Petauristinae Miller, 1912

Petauristodon Engesser, 1979

? *Petauristodon* sp.

(Fig. 2I)

Referred Specimen.—UNSM 101659, left M₃.

Measurements.—a-p, 3.62 mm; tra, 3.59 mm; trp, 3.10 mm.

Table 3.—Dental measurements of *Ammospermophilus junturensis*. Abbreviations as in Table 1. Measurements of holotype taken from Black (1963:226). Measurements in mm.

UNSM No.	P ₄		M ₁			M ₂			M ₃			P ₃		M ¹ or M ²		
	a-p	tra	tp	a-p	tra	tp	a-p	tra	tp	a-p	tra	tp	a-p	tr	a-p	tr
101755	1.23	0.90	1.24													
101756	1.37	0.99	1.14													
101757				1.68	—	1.90										
101578				1.66	1.81	1.63										
101759				1.61	1.63	1.79	1.74	2.01	1.95							
101760				1.85	1.88	1.85										
101761				1.63	1.70	1.83										
101762							1.60	1.35	1.14						1.87	2.41
101763							2.22	1.96	1.74						1.86	2.38
101764							2.28	2.07	1.81						1.76	2.21
101751										0.78	0.82				1.94	—
101592																
101752																
101753																
101754																
UOMNH No. (holotype)																
F-5871	1.30	1.05	1.45	1.55	1.60	1.80	1.75	1.85	1.90	2.00	1.95	1.90				

Description and Discussion.—The isolated specimen referred here to *Petauristodon* varies from those of other species of the genus only in its larger size and less prominent crenulations in the talonid basin of the tooth (James, 1963; Lindsay, 1972; Engesser, 1979). If better represented, the Pratt Quarry specimen might well represent a new species.

Sciurion Skwara, 1986

cf. *Sciurion* sp.

(Fig. 2J)

Referred Specimen.—UNSM 101769, isolated left M_1 or M_2 .

Measurements.—a-p, 1.42 mm; tra, 1.50 mm; trp, 1.56 mm.

Description.—The single lower molar is smaller than all of the other sciurids from Pratt Quarry. It is rhomboid, with no evidence of the anteroposterior compression present in the molars of *Ammodontomys* and *Spermophilus*. There are faint enamel wrinkles in the talonid and trigonid basins. The metalophulid I runs from the apex of the metaconid along the anterior border of the tooth, ending in a distinct cuspule (= anterostylid) anterior and lingual to the protoconid. The trigonid basin is small and blocked posteriorly by a complete but low metalophulid II. The ectolophid is low and obliquely oriented with just a trace of a mesoconid. The posterolophid is continuous from the hypoconid to the entoconid. The entoconid is distinct and round, not compressed into the lingual end of the posterolophid as in the spermophiles. A small mesostylid is present posterior to the metaconid.

Discussion.—*Sciurion campestre* was named from the Hemingfordian of Saskatchewan (Skwara, 1986). The Pratt Quarry specimen differs from the type material in having a complete metalophulid II and less well-defined mesoconid. UNSM 101769 is also larger than the referred lower molar of *S. campestre* (Skwara, 1986:table 1). In size, UNSM 101769 is close to the European *Blackia*. *Blackia* was originally named for a small “flying squirrel” from the Miocene of Europe (Mein, 1970). UNSM 101769 differs from the described species of *Blackia* from Europe in having less pronounced wrinkling of the enamel on the cheek teeth, a complete metalophulid II, and a more distinct entoconid, mesostylid, and anterostylid.

The only occurrence of *Blackia* in North America is based on several isolated teeth from the Hemingfordian of California (Hutchison and Lindsay, 1974) and the medial Barstovian of Nebraska (Voorhies, 1990b). The Pratt Quarry specimen is slightly smaller than the Barstovian lower molar from Nebraska (UNSM 85558) and has a complete metalophulid II (trigonid completely open in the Barstovian specimen) and a better developed entoconid, mesoconid, and mesostylid. The Pratt Quarry specimen differs from the Hemingfordian specimens in being larger and the features discussed by Skwara (1986) for *S. campestre*.

Family Castoridae Gray, 1821

Subfamily Castoroidinae Trouessart, 1880

Dipoides Jager, 1835

Dipoides tanneri, new species

(Fig. 3, 4, 5A–C, Table 4)

Type Specimen.—UNSM 101612, little worn P_4 .

Referred Specimens.—UNSM 101613–101620, P_4 ; UNSM 101621–101631, P^4 ; UNSM 101632–101653, 101795, 101798, FAM 64483–64487, isolated molars; UNSM 101654–101657, isolated incisors; UNSM 101730, distal humerus; UNSM 101731, proximal femur; FAM 64488, 64517, mandibles with P_4 – M_2 ; FAM 64482, complete skull with associated mandible and postcranial elements.

Diagnosis.—Similar in size to *D. stirtoni*; differs from all other species of the genus in the lower crown height of the cheek teeth (premolars develop roots in

very late stages of wear), upper premolars not attaining the S-pattern of the occlusal surface, and the lower premolar having a parastridium shorter than the mesostriid (parastridium not reaching the base of the tooth) as in *D. stirtoni*, and a small metafossettid retained until very late stages of wear (absent in other species).

Eymology.—Patronym for Lloyd Tanner, in recognition of his many years of work for the UNSM.

Description.—The nearly complete skull with heavily worn dentition (FAM 64482) lacks only parts of the zygomatic arches. Due to the advanced age of the individual, some of the cranial sutures are not distinguishable. Also, damage to the pterygoid and basicranial area has obscured the features and foramina of this area. In general shape, it is not as deep dorsoventrally as the skull of Recent *Castor*, and the rostrum is relatively longer. Wahlert (1972) fully described the skull of a Hemphillian *Dipoides* and noted only four differences in the cranial foramina between *Dipoides* and earlier *Eucastor* and *Monosaulax*: 1) posterior palatine foramina medial to M¹ in *Dipoides*, medial to the boundary of M¹ and M² in the other genera; 2) lateral margin of the infraorbital foramen forms part of the masseteric tubercle in *Dipoides* but continues into the tubercle in the other genera; 3) the sphenopalatine foramen is dorsal to the premolar in *Dipoides* and more posterior in the other genera; and 4) the ethmoid foramen is entirely within the frontal bone in *Dipoides* and passes through the frontal-orbitosphenoid suture in the other genera. Nearly complete skulls of *E. tortus* from the Valentine Formation of Nebraska (UNSM 85600) and *M. pansus* from New Mexico (FAM 64945) were compared with FAM 64482. All of the differences cited by Wahlert (1972) hold true for the skull of *D. tanneri* except for the morphology of the infraorbital foramen. In the skull of *D. tanneri* the foramen continues into the masseteric tubercle as in *Eucastor* and *Monosaulax*. Other than these differences, there is little distinction between the skulls of these three beavers.

One other feature of the cranial foramina of the Hemphillian *Dipoides* figured by Wahlert (1972: fig. 16) is the presence of three interorbital foramina posterior and ventral to the optic foramen. In the specimens of *Eucastor* and *Monosaulax* at hand, there are only two interorbital foramina. The skull of *D. tanneri* has three foramina as in the Hemphillian *Dipoides*. In size, the skull of *D. tanneri* is at least 50% larger than the skulls of the other two beavers.

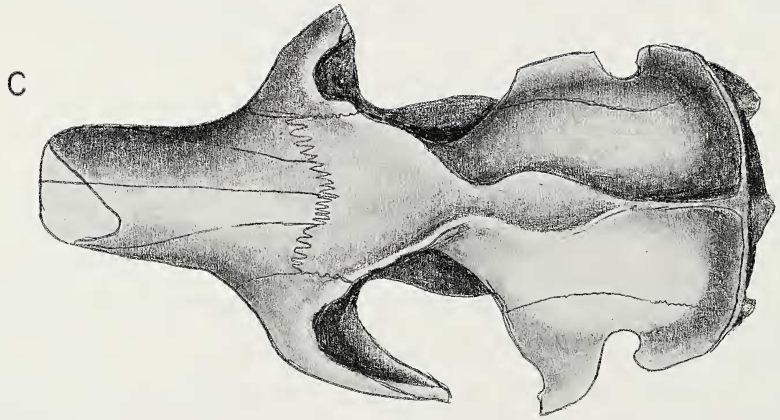
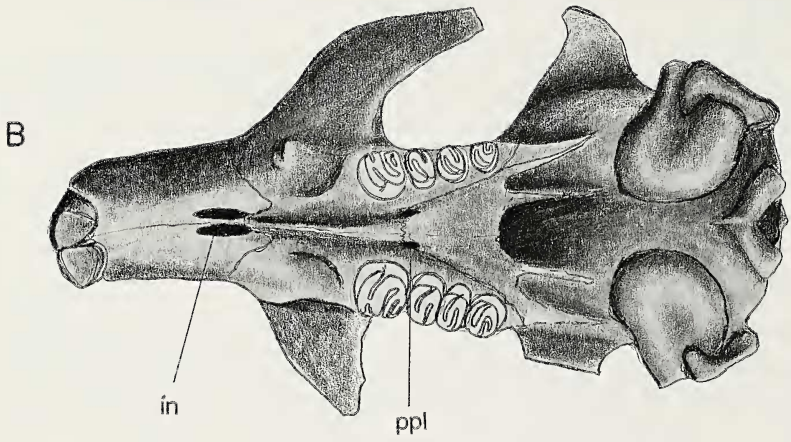
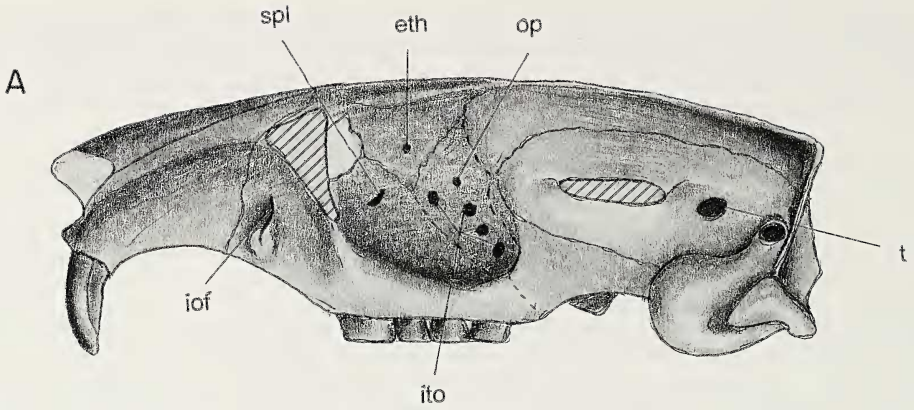
The molars of *D. tanneri* are hypsodont and rootless. The occlusal patterns of both the upper and lower molars quickly wear to the characteristic S-pattern of *Dipoides*. The flexi remain open and do not close to form fossettes (-ids) until the latest stages of wear.

M³ is distinct from the anterior molars. It does not taper towards the base of the crown. On the buccal side of the tooth, there is only one persistent stria, the mesostria. The parastridium is much shorter, and a parafossette is formed after only moderate wear. The hypostria is continuous to the base of the crown and the hypoflexus is as in the anterior molars. In late stages of wear the parafossette is lost and the hypoflexus extends to the buccal margin of the tooth. On little-worn specimens there is a short metastridium. The metaflexus and mesoflexus isolate the metacone. After the metastridium has been worn away, the metacone remains isolated. The mesoflexus extends to the lingual margin of the tooth and is strongly concave posteriorly.

The premolars of *D. tanneri* develop roots only in the very late stages of wear. On the lower premolars, the buccal hypostriid and lingual mesostriid are continuous to the base of the crown, thus the hypoflexid and mesoflexid remain open throughout the life of the individual. The parastridium is slightly shorter than the mesostriid, ending only a few millimeters from the base of the crown. Because of the length of the parastridium, in very late stages of wear, the paraflexid closes lingually to form a parafossettid. In occlusal view, the paraflexid, mesoflexid, and hypoflexid are all concave anteriorly and cross nearly the entire width of the tooth. The only variation is the presence of a small metafossettid at the lingual end of the hypoflexid. This metafossettid is present on all specimens except those with extreme wear.

The upper premolars are square in occlusal outline and the crown is strongly curved (concave buccally). On the lingual side of the tooth, the hypostria is continuous to the base of the crown. On the buccal side, the parastridium and mesostria extend to within 2–4 mm of the base of the crown, but the metastridium extends less than half of the height of the crown toward the base of the crown. On the occlusal surface of the tooth, the hypoflexus and paraflexus meet on the buccal half of the tooth, being separated only by a thin enamel wall. The mesoflexus extends to the lingual border of the tooth. The metaflexus is only about half the tooth in length and closes off buccally after only moderate wear to form a small fossette. All of the flexi on P⁴ are concave posteriorly.

Discussion.—*Dipoides tanneri* is referable to this genus based on Stirton's (1935:440) diagnosis—high-crowned cheek teeth with striae (-ids) persistent to the base of the crowns. The skull of *D. tanneri* also has the distinctive features



of *Dipoides*, not present in *Eucastor* (posterior palatine foramina more anterior, ethmoid foramen entirely within the frontal bone, three interorbital foramina present posterior and ventral to the optic foramen, and the sphenopalatine foramen more anteriorly positioned).

Dipoides tanneri is clearly distinguishable from contemporaneous species of *Eucastor* because of these differences. The Clarendonian *Eucastor malheurensis* is similar to *D. tanneri* in crown height of the cheek teeth, but is much smaller than *D. tanneri* (Shotwell and Russell, 1963:table 8) and the striae (-ids) of the cheek teeth do not extend as far toward the bases of the crowns, thus forming fossettes (-ids) earlier in wear. Two species of *Eucastor* have been identified from the Clarendonian of the Great Plains, *E. dividerus* from Nebraska (Webb, 1969a) and *E. philisi* from Kansas (Wilson, 1968). Both of these species are similar in size to *D. tanneri* but do not have the persistent striae (-ids) of the cheek teeth of *D. tanneri* (Stirton, 1935:fig. 107–110; Wilson, 1968:text-fig. 15).

Dipoides tanneri differs from all other species of *Dipoides* in having lower-crowned cheek teeth, maintaining a metafossettid on P_4 until late stages of wear, having roots develop on the premolars in late stages of wear, having P^4 and M^3 not attain the S-pattern of the other molars, and having the parastridium shorter than the mesostridium on P_4 . All of these features are viewed as primitive and are shared with species of *Eucastor*.

Among species of *Dipoides*, *D. tanneri* most closely resembles *D. stirtoni* from the early Hemphillian of Oregon (Wilson, 1934). *Dipoides stirtoni*, like *D. tanneri* has a P_4 with a shorter parastridium than mesostridium. In all other species both of these stridiums extend to the base of the crown. Similarly, P^4 and M^3 of *D. stirtoni* do not wear to the occlusal S-pattern characteristic of *Dipoides*. *Dipoides tanneri* differs from *D. stirtoni* in having lower-crowned cheek teeth and developing roots on the premolars. The postcranial material assigned to *D. tanneri* differs from that of *D. stirtoni* only in being slightly smaller and less robust (Wilson, 1934: fig. 1).

Dipoides tanneri is the earliest occurrence of the genus. All other species of *Dipoides* are known only from the Hemphillian and Blancan (Korth, 1994:148). This earlier occurrence is compatible with the more primitive features of the dentition of *D. tanneri*.

Eucastor Leidy, 1858

Eucastor planus Stirton, 1935

(Fig. 5D–F, Table 5)

Referred Specimens.—UNSM 101594, partial mandible with incisor and P_4 – M_1 ; UNSM 101610, I_1 ; UNSM 101611, P_4 ; UNSM 101596, 101600, 101602, 101605, 101607–101609, 101611, 101658, M_1 or M_2 ; UNSM 101603, M_3 ; UNSM 101597, 101601, 101604, P^4 ; UNSM 101595, 101606, 101794, M^1 or M^2 ; UNSM 101598, 101599, M^3 .

Discussion.—The specimens referred here to *Eucastor planus* do not differ from the holotype from the Clarendonian of Oklahoma (Stirton, 1935) or other

←

Fig. 3.—Skull of *Dipoides tanneri*, FAM 64482. A, lateral view (zygoma removed). B, ventral view. C, dorsal view. Abbreviations of foramina: eth, ethmoid; iof, infraorbital; in, incisive; ito, interorbital; op, optic; pgl, postglenoid; ppl, posterior palatine; spl, sphenopalatine. Bar scale = 1 cm. Dashed lines indicate probable orientation of sutures.

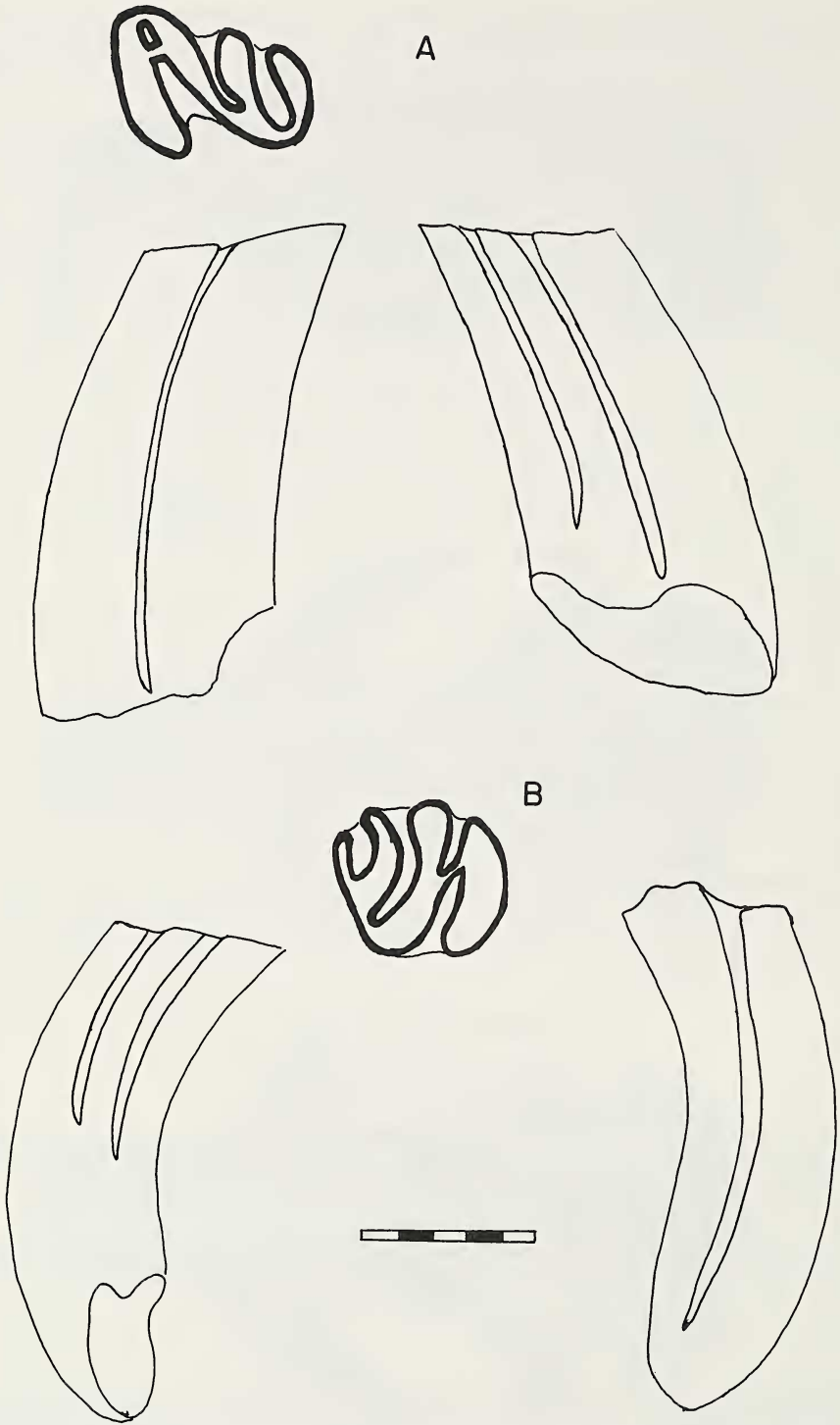


Fig. 4.—Unworn premolars of *Dipoides tanneri*. A, UNSM 101612, holotype, right P₄; occlusal view (above), buccal view (left), and lingual view (right). B, UNSM 101628, right P₄; occlusal view (above), buccal view (left), and lingual view (right). Bar scale = 5 mm.

Table 4.—Dental measurements of *Dipoides tanneri*. Abbreviations as in Table 1. Crown height measured only on unworn or little worn lower premolars. Measurements in mm.

		Isolated premolars						
		<i>n</i>	M	OR	<i>s</i>	CV		
P ₄	a-p	9	7.03	6.48–7.86	0.50	7.1		
	tra	8	3.92	3.49–4.55	0.40	10.2		
	trp	9	4.69	3.98–5.38	0.41	8.7		
	crown height	5	14.20	13.40–15.60	0.85	6.0		
P ⁴	a-p	11	4.47	3.92–5.01	0.29	6.5		
	tr	11	5.22	4.70–5.59	0.29	5.6		
		Teeth in jaws						
		FAM No.			FAM No.			
		64482	64488	64517	64482	(Left)	(Right)	
P ₄	a-p	6.28	6.10	6.39	P ⁴	a-p	6.10	6.31
	tra	4.41	4.10	4.40		tr	5.78	5.52
	trp	5.02	5.35	5.21				
M ₁	a-p	4.59	4.14	4.30	M ¹	a-p	3.90	3.81
	tr	4.80	5.09	4.88		tr	4.58	5.15
M ₂	a-p	3.40	3.82	4.25	M ²	a-p	3.87	3.80
	tr	4.39	5.01	4.64		tr	4.99	5.20
M ₃	a-p	4.76			M ³	a-p	4.49	4.25
	tr	4.00				tr	3.93	4.29
P ₄ –M ₃		19.79	20.10	19.88	P ⁴ –M ³		19.22	18.37

referred specimens of this species. This species is clearly separable from the other castorids from Pratt Quarry by its markedly smaller size, having higher-crowned cheek teeth than *Hystricops*, and having less well-developed striae (-ids) on the cheek teeth than in *Dipoides*. *Eucastor planus* has previously been identified in the early Clarendonian Burge and medial Clarendonian Minnechaduzza faunas of northcentral Nebraska as well (Webb, 1969a; Voorhies, 1990a).

Subfamily uncertain

Hystricops Leidy, 1858

Hystricops venustus Leidy, 1858

(Fig. 6, Table 6)

Hystrix (Hystricops) venustus Leidy, 1858.

Hystrix venustus Leidy, 1869.

Erethizon venustus (Leidy) Hay, 1901.

Hystricops venustus Leidy: Stirton, 1935.

Referred Specimens.—UNSM 101660, P₄; UNSM 101661, 101662, 101775, M₁ or M₂; UNSM 101663, 101664, 101667, M₃; UNSM 101655, 101666, P⁴; UNSM 101668, 101669, upper molars; UNSM 101747, incisor fragment.

Description.—The cheek teeth are mesodont and strongly rooted, much lower crowned than the other castorids from Pratt Quarry, and clearly much larger in size (Table 6). One incisor fragment is preserved, UNSM 101747. It has a broad, gently convex, and smooth anterior surface.

The lower premolar is the largest of the cheek teeth. It has two roots. The only striids that are continuous to near the base of the crown are the hypostriid and the mesostriid. All others are very short, disappearing after only moderate wear. The mesoflexid is the longest of the flexids, extending nearly to the buccal edge of the tooth. The mesoflexid is gently curved anteriorly. The hypoflexid is much shorter, extending only about one-fourth the width of the tooth, posterior to the mesoflexid, in

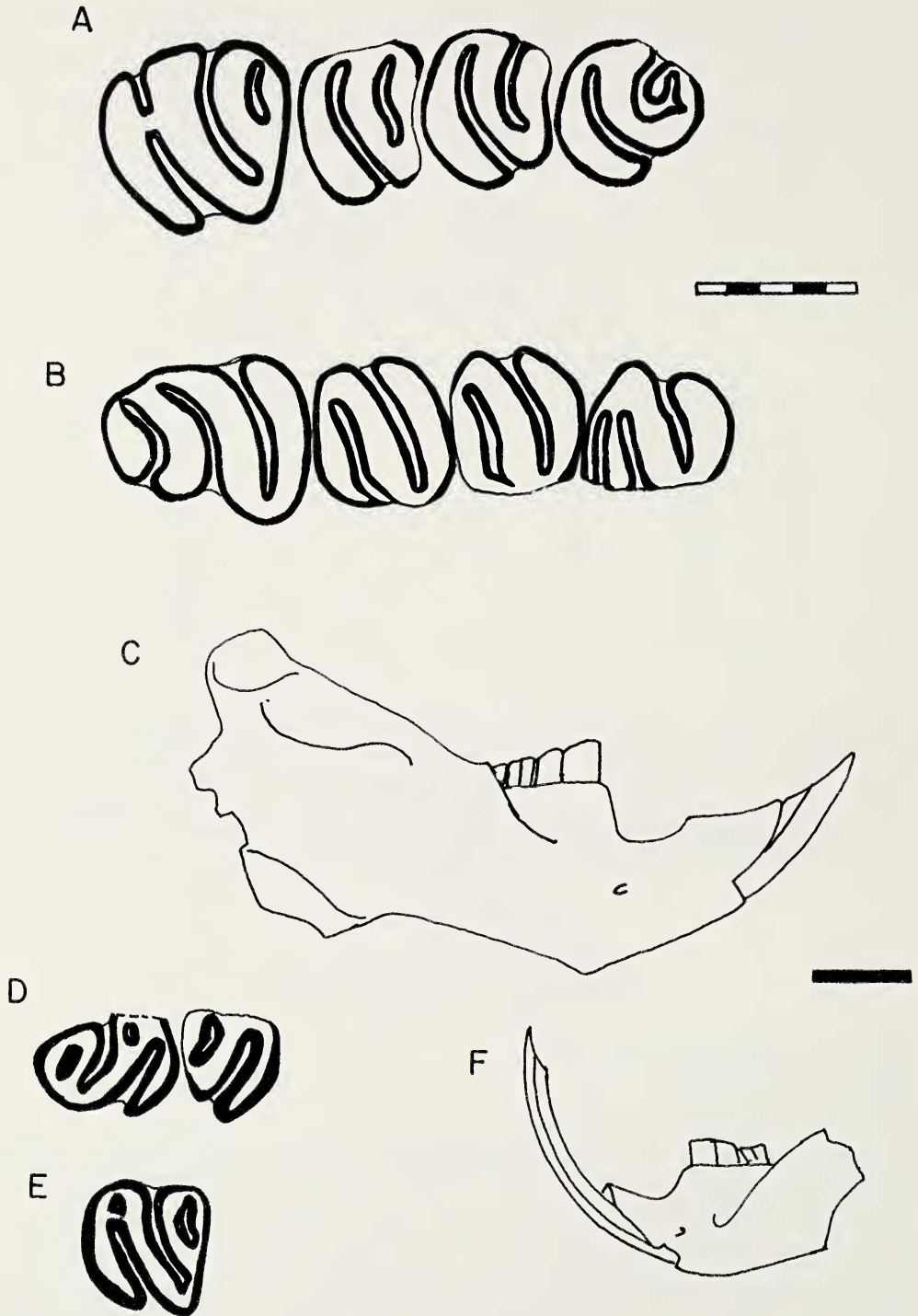


Fig. 5.—Cheek teeth and mandibles of castorids from Pratt Quarry. A–C, *Dipoides tanneri* FAM 64482. A, left P⁴–M³. B, right P₄–M₃. C, lateral view of mandible. D–F, *Eucastor planus*. D, UNSM 101594, left P₄–M₁. E, UNSM 101609, left P⁴. F, UNSM 101594, lateral view of mandible. Bar scale for teeth (above) = 5 mm. Bar scale for mandibles (below) = 1 cm.

Table 5.—Dental measurements of *Eucastor planus* from Pratt Quarry. Abbreviations as in Table 1. Measurements in mm.

		<i>n</i>	M	OR	<i>s</i>	CV
P ₄	a-p	2	4.40	4.27–4.52		
	tra	2	2.84	2.70–2.98		
	trp	2	3.47	3.34–3.60		
M ₁ or M ₂	a-p	8	3.10	2.72–3.51	0.32	10.2
	tr	8	3.74	3.02–4.09	0.42	11.6
M ₃	a-p	1	2.50			
	tr	1	2.89			
P ⁴	a-p	3	3.64	3.51–3.80	0.15	4.0
	tr	3	4.01	3.46–4.36	0.48	12.0
M ¹ or M ²	a-p	2	3.09	3.00–3.18		
	tr	2	3.60	3.50–3.60		
M ³	a-p	2	2.74	2.67–2.80		
	tr	2	2.63	2.41–2.85		

a posterolingual direction. On the anterior half of the tooth is a large, anteriorly concave parafossettid. Irregularities of the enamel are preserved along its borders. Anterior to the parafossettid is a much smaller fossettid that is straight and oriented transversely. Along the lingual border of the tooth between the mesoflexid and the parafossettid is a short flexid that is oriented posterobuccally. The associated striid on the lingual side of the tooth is very short (approximately one-eighth the remaining crown height) and would soon disappear after only a little more wear. The posterior half of the tooth is dominated by a transversely elongated hypofossettid. There are two bends in the hypofossettid, giving it a zig-zag shape. Posterior and lingual to the hypofossettid is a minute fossettid that is oriented obliquely.

The anterior lower molars are three-rooted, with one posterior and two smaller anterior roots. They are nearly square in occlusal outline. Only one flexid, the hypoflexid, remains open to near the base of the crown. On all other specimens the only lingual flexid is the mesoflexid on one specimen (UNSM 101775). There is no evidence of the parafossettid or metafossettid communication with the lingual margin of the tooth on any of the available specimens. The parafossettid is transversely elongated and the only fossettid on the anterior half of the tooth. It has several subtle bends in it, giving it an irregular shape. In one specimen, UNSM 101661, the buccal end of the parafossettid is separated from the rest of the fossettid, and forms a small, obliquely oriented fossettid. The mesofossettid is straight and extends a little over half of the width of the tooth. It is oriented slightly anterobuccally. The hypoflexid extends about half the width of the tooth and is posterolingually oriented, paralleling the mesofossettid. A short metafossettid is the only feature of the posterior half of the tooth. It is mostly parallel with the mesofossettid, but has a bend near its buccal end, similar to the metafossettid in P₄.

The last lower molar is essentially identical to the anterior molars except it is narrower and longer.

P⁴ is the largest of the upper cheek teeth. The only persistent flexus is the hypoflexus, the hypostria extending nearly to the base of the crown. On UNSM 101666 the mesoflexus has remained open, but the mesostris extends less than one-fourth of the remainder of the crown height, indicating that the flexus would close after only a little more wear. There is no indication of a parastris or metastris on either of the available specimens. The hypoflexus is oriented in an anterobuccal direction and extends about one-third the width of the tooth. Its buccal end abuts the lingual end of the parafossette. The parafossette follows the direction of the hypofossette, is transversely elongated, and retains some minor irregularities along its enamel outline. On UNSM 101666 there is a minute enamel fossette anterior to the parafossette. It appears that this accessory fossette would erode after only a little more wear. The mesofossette (or mesoflexus) extends nearly the entire width of the tooth and curves posteriorly, ending along the posterior margin of the tooth. The metafossette is short and obliquely oriented.

The upper molars are similar to P⁴ in occlusal pattern but smaller in size, being greatly shortened anteroposteriorly. There is no evidence of buccal striae on any of the referred upper molars. The mesofossette is long, posteriorly curved, and meets the posterior wall of the tooth. The parafossette and metafossette are small and placed as in P⁴. The hypoflexus, again, is oriented as in P⁴.

Discussion.—The type specimen of *Hystricops venustus* is an isolated lower premolar and lower molar, USNM 1180, from the “Niobrara River fauna” of northcentral Nebraska (Leidy, 1858; Sturton, 1935). The single P₄ from Pratt Quar-

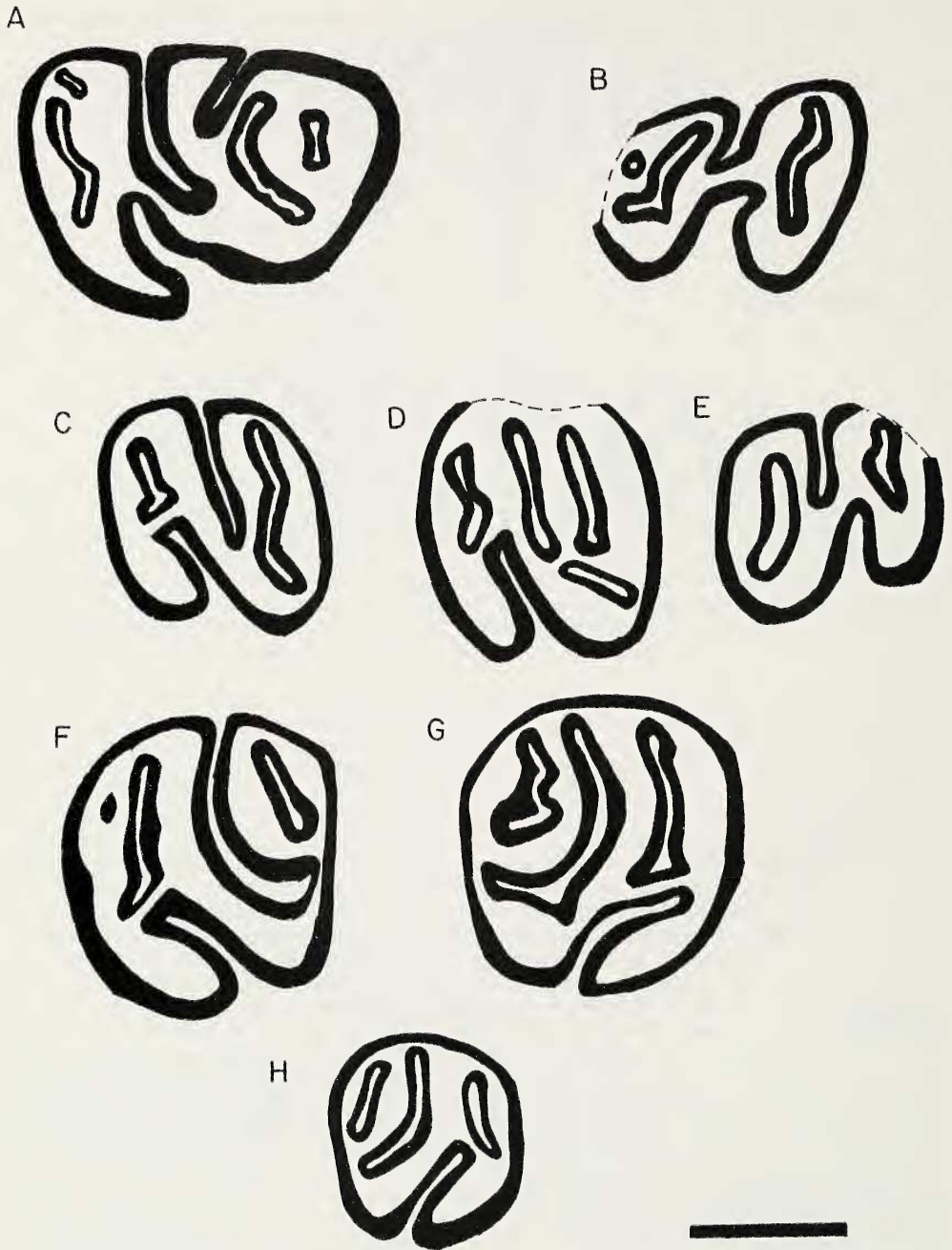


Fig. 6.—Cheek teeth of *Hystricops venustus*. A, UNSM 101660, right P₄. B, holotype, USNM 1180, left P₄. C, UNSM 101775, right M₁ or M₂. D, UNSM 101661, right M₁ or M₂. E, UNSM 101667, left M₃. F, UNSM 101666, left P⁴. G, UNSM 101665, right P⁴. H, UNSM 101668, right M¹ or M². Bar scale = 5 mm.

Table 6.—Dental measurements of *Hystricops venustus* from Pratt Quarry. Abbreviations as in Table 1. Measurements in mm.

UNSM No.	Isolated Cheek Teeth													
	P ₄			M ₁ or M ₂			M ₃			P ^a			M ^l	
	a-p	tra	trp	a-p	tra	trp	a-p	tra	trp	a-p	tra	trp	a-p	tr
101660	11.90	7.65	9.11											
101661				7.59	8.14	8.33								
101662				8.00	8.00	7.33								
101775				7.45	8.01	7.14								
101663							7.35	6.51	6.16					
101664							—	5.80	5.84					
101667							5.86	5.80	5.68					
101665										8.50	9.39	8.82		
101666										8.42	9.42	8.65		
101668													6.32	6.51
101669													5.74	7.00

ry (UNSM 101660) is similar in size to the holotype premolar and differs only in the presence of a small reentrant valley on the lingual side of the tooth anterior to the mesoflexid and the minute accessory fossettid lingual to the metafossettid. It appears that this accessory valley and the accessory fossettid would be worn away after only slightly more wear. This is evident on the short flexid because there is no striid on the lingual side of the tooth continuous with it. The remainder of the occlusal morphology is nearly identical with the holotype.

The lower molars referred here to *H. venustus* have all of the lingual flexids closed early in wear, and are nearly identical to the isolated molar included in the holotype of *H. venustus* (Stirton, 1935:fig. 60). The reference of the Pratt Quarry material to *H. venustus* is almost certain. There are no known castorids of this size and morphology reported from the lower horizons (medial to late Barstovian) in the Niobrara River valley of northcentral Nebraska, even though they have been extensively collected and described (Voorhies, 1990b).

The morphology of the upper premolars is also nearly identical to the unnamed species of *Hystricops* reported from the Clarendonian of Oregon (Shotwell and Russell, 1963). The Hemphillian *H. browni* from Oregon (Shotwell, 1963) is also similar in occlusal morphology to the upper premolars referred to *H. venustus* from Pratt Quarry, but differs in the depth of the striae. This similarity verifies the assignment of these later Tertiary beavers to *Hystricops*.

There is also a great similarity in the morphology of the cheek teeth of *H. venustus* to those of an unnamed castorid from the Hemingfordian of Colorado referred by Wilson (1960) to *?Anchitheriomys* sp. (KU 10173). It appears that the Colorado specimen is also referable to *Hystricops* rather than *Anchitheriomys*. Some of the skull characters of the Colorado skull also differ from those of *Anchitheriomys* (Korth and Emry, 1997). Dorsally, the nasals extend farther posteriorly than the premaxillary bones, a character only otherwise present in *Agnotocastor* and *Neotocastor* among castorids (Korth, 1996a). Likewise, the rostrum is more elongated than in typical castorids, another feature of *Agnotocastor* and *Neotocastor*.

Besides being referable to *Hystricops*, the Hemingfordian skull from Colorado appears to relate this genus to the *Agnotocastorinae* (Korth, 1996a; Korth and

Emry, 1997). However, a detailed description and study of the Colorado specimen is necessary before such an allocation can be made.

Family Eomyidae Deperet and Douxami, 1902

Pseudotheridomys Schlosser, 1926

cf. *Pseudotheridomys* sp.

(Fig. 8A)

Referred Specimen.—UNSM 101748, right mandible with fragment of lower incisor and alveoli for all cheek teeth.

Description.—The mandible is small (alveolar length of cheek teeth = 3.5 mm) and nearly complete, lacking only the base and the posterior processes (coronoid, condyle, and angle). There are alveoli for four cheek teeth: the premolar was two-rooted and the molars three-rooted (one posterior, two anterior). The masseteric scar ends anteriorly below the anterior root of the premolar in a V-shape. On the ascending ramus, the base of the incisor is a lateral bulge that tapers posteriorly to a small ridge. The diastema is shorter than the tooth row and concave. The mental foramen is near the dorsoventral center of the mandible, below the center of the diastema.

Discussion.—Only three genera of eomyids persist in North America into the Barstovian and later times—*Leptodontomys*, *Kansasimys*, and *Pseudotheridomys* (Korth, 1994:161). Of these only *Leptodontomys* and *Pseudotheridomys* are similar in size to UNSM 101748 from Pratt Quarry. UNSM 101748 most closely resembles the mandible of *Pseudotheridomys* because of the more anterior extent of the masseteric scar, shorter diastema, morphology of the base of the incisor on the ascending ramus (low, shelf-like structure on *Leptodontomys*), and the alignment of the alveolar margin of the cheek teeth with the alveolus of the incisor. Engesser (1979:fig. 7a) described the mandible of *Leptodontomys* in detail and noted that the alveolar margin of the cheek teeth generated a line that, if extended anteriorly, would pass the incisor well above its alveolus. In UNSM 101748 and other species of *Pseudotheridomys* this line would be level with the incisor alveolus.

In size, UNSM 101748 is nearly identical to *P. pagei* from the Barstovian of Oregon (Shotwell, 1967a). However, the lack of cheek teeth does not allow a for a definite specific identification of the Pratt Quarry specimen.

Previously, the last reported occurrence of *Pseudotheridomys* in North America was the Barstovian (Engesser, 1979; Fahlbusch, 1979). The recognition of this genus in the late Clarendonian greatly extends its record in North America. In Europe, *Pseudotheridomys* disappears even earlier in the fossil record (Fahlbusch, 1979). Because UNSM 191748 was recovered from the base of the channel at Pratt Quarry, it is possible that it is reworked from the Barstovian layers of the Valentine Formation below the channel. However, there is no previous record of *Pseudotheridomys* from the Valentine Formation (Klingener, 1968; Korth, 1979; Voorhies, 1990b).

Family Heteromyidae Gray, 1868

Subfamily Mioheteromyinae Korth, 1997

Mioheteromys Korth, 1997

Mioheteromys sp., cf. *M. agrarius* (Wood, 1935)

(Fig. 7A, 8B)

Referred Specimens.—UNSM 101750, isolated P⁴; UNSM 101573, partial mandible with lower incisor.

Measurements.—UNSM 101750, a-p, 1.67 mm; tra 0.96 mm; trp, 1.56 mm.

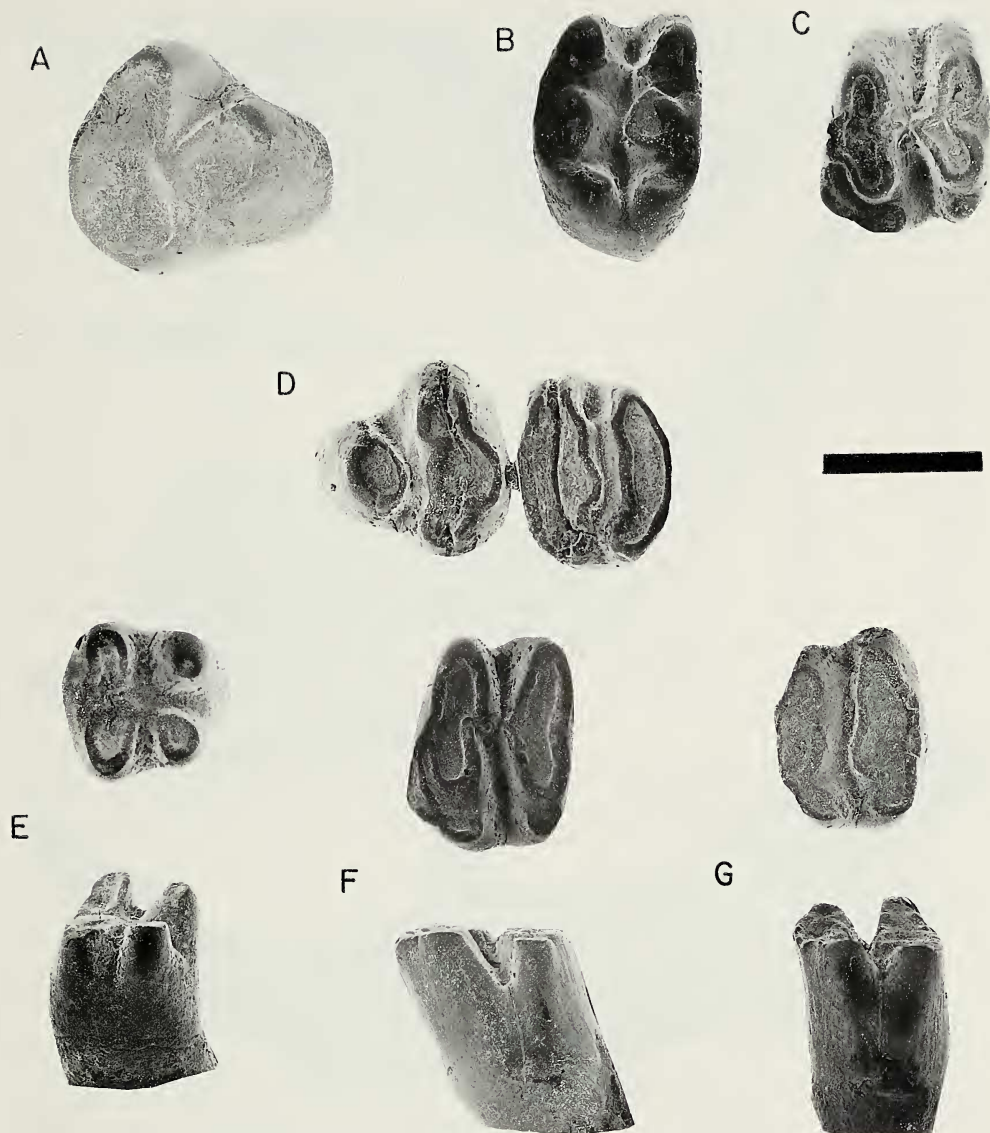


Fig. 7.—Scanning electron micrographs of cheek teeth of heteromyid rodents from Pratt Quarry. A, *Mioheteromys* sp., cf. *M. agrarius*, right P⁴, UNSM 101750. B, C, *Lignimus* sp. B, right M¹ or M², UNSM 101576. C, left M¹ or M², UNSM 101531. D–G, *Cupidininus prattensis*. D, left P⁴–M¹, UNSM 101502. E, Holotype, left P₄ (occlusal view above, lingual view below), UNSM 101501. F, left M¹ or M² (occlusal view above, buccal view below), UNSM 101512. G, right M¹ or M² (occlusal view above, lingual view below), UNSM 101510. Bar scale = 1 mm.

Discussion.—A single isolated heteromyid P⁴ is distinct from the *Cupidininus* specimens from Pratt Quarry because of its larger size and lower crown height. The union of the protocone to the metaloph is also lingual rather than central as in *Cupidininus*. All of these distinctive characters are typical of *Mioheteromys*. The size of the specimen is comparable with P⁴s of *M. agrarius* from the early and middle Clarendonian of Nebraska (Korth, 1997).

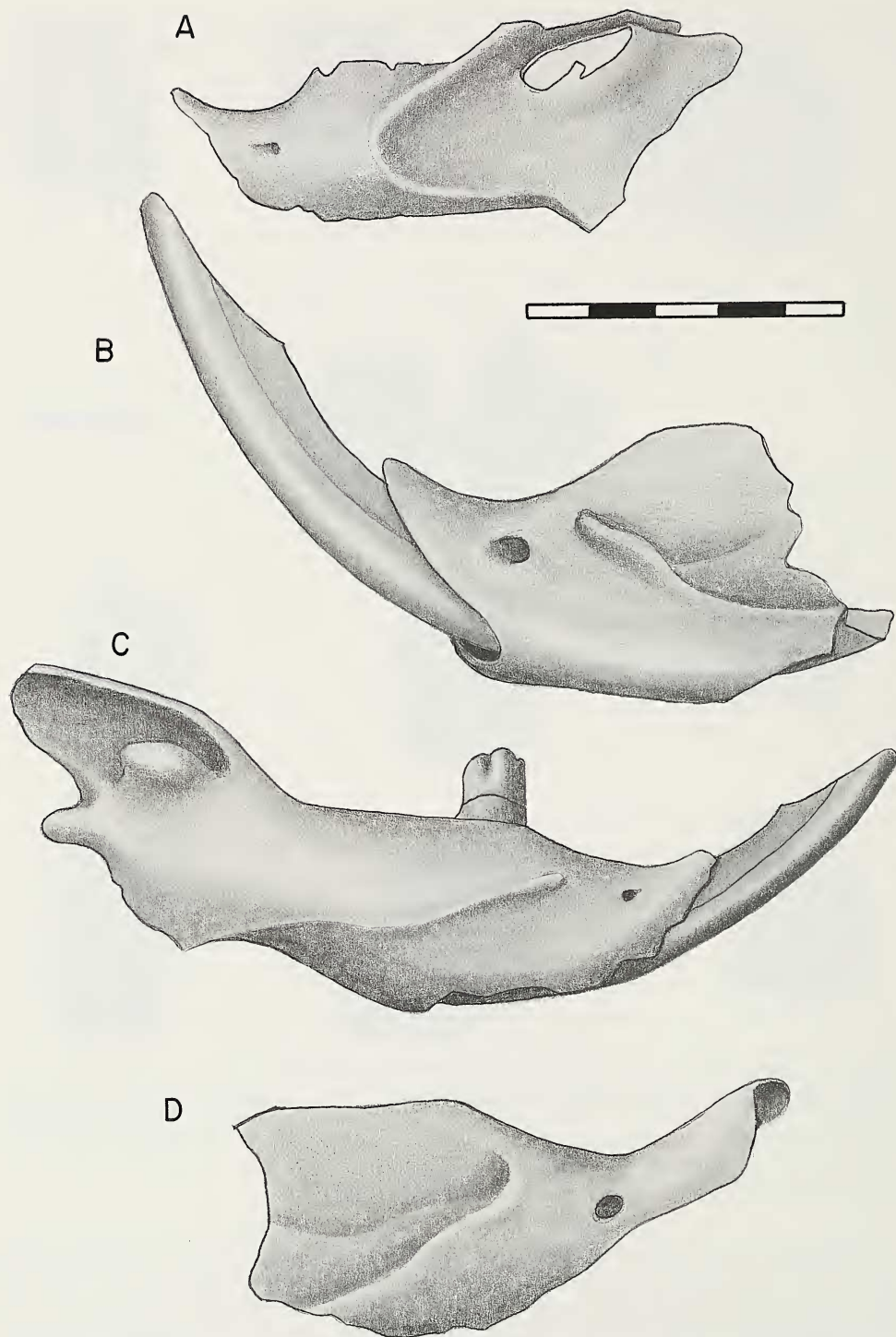


Fig. 8.—Mandibles of geomyoids from Pratt Quarry. All lateral views. A, cf. *Pseudotheridomys* sp., UNSM 101748. B, *Mioheteromys* sp., cf. *M. agrarius*. C, *Cupidinimus prattensis*, holotype, UNSM 101501. D, *Lignimus* sp., UNSM 101532. Bar scale = 5 mm.

Table 7.—Dental measurements of *Cupidinimus prattensis*. Abbreviations as in Table 1. Additional abbreviations (crown height variables from Barnosky, 1986a): CHEV, height of enamel chevron on lingual side of upper molars; LEH, buccal enamel height of lower molars; LEHP, buccal enamel height of lower premolar; T, maximum transverse width; TOH, crown height of lingual side of upper molars; TP, transverse width of P₄.

		<i>n</i>	M	OR	<i>s</i>	CV
P ₄	a-p	1	0.91			
	tra	1	0.84			
	trp	1	0.91			
	LEHP	1	0.48			
	LEHP/TP	1	0.53			
M ₁ or M ₂	a-p	4	1.15	0.98–1.26	0.12	10.4
	tra	4	1.44	1.33–1.59	0.11	7.7
	trp	4	1.34	1.24–1.49	0.11	8.1
	LEH	3	0.65	0.54–0.73	0.10	16.1
	LEH/T	3	0.44	0.38–0.47	0.05	11.3
P ⁴	a-p	11	1.41	1.28–1.55	0.10	7.0
	tra	11	0.75	0.67–0.83	0.04	6.0
	trp	11	1.33	1.20–1.43	0.08	6.2
M ¹ or M ²	a-p	7	1.06	0.95–1.24	0.10	9.8
	tra	7	1.32	1.16–1.43	0.10	7.7
	trp	7	1.26	1.15–1.34	0.07	5.5
	CHEV	7	0.19	0.13–0.28	0.06	30.4
	TOTH	6	0.88	0.73–0.97	0.09	10.7
	CHEV/T	7	0.14	0.09–0.23	0.05	33.9
	TOTH/T	6	0.64	0.53–0.70	0.06	9.7

The partial mandible preserves the alveoli for P₄ and M₁ only. The rest of the mandible posterior to M₁ is missing. It does not differ from the mandible of *M. agrarius* described previously (Wood, 1935; Korth, 1997).

Subfamily Dipodomysinae Gervais, 1853

Cupidinimus Wood, 1935

Cupidinimus prattensis, new species

(Fig. 7D–G, 8C; Table 7)

Type Specimen.—UNSM 101501, right mandible with I₁ and P₄.

Referred Specimens.—UNSM 101502, maxilla with P⁴–M¹; UNSM 101528, edentulous maxilla; UNSM 101503–101509, 101513, 101519, 101521, isolated P⁴; UNSM 101510, 101511, 101514, 101515, 101520, isolated M¹ or M²; UNSM 101512, 101517, 101529, 101530, isolated M₁ or M₂; UNSM 101522–101527, mandibles lacking cheek teeth.

Diagnosis.—Intermediate sized, smaller than *C. kleinfelderi*, *C. avawatzensis*, *C. quartus*, and *C. bidahochiensis*, larger than *C. eurekensis* and *C. lindsayi*; lower crowned than *C. nebraskensis*, *C. whitlocki*, and *C. halli*, higher crowned than *C. kleinfelderi*, *C. boronensis* and *C. smaragdinus* with better-developed enamel chevrons on upper molars; also differs from *C. whitlocki* in having a relatively longer P⁴; differs from *C. saskatchewanensis* in lacking the central anteroposterior loph on P₄; differs from *C. tertius* and *C. cuyamensis* in lacking accessory cusps on protoloph of P⁴; differs from *C. nebraskensis* and *C. madisonensis* in having M¹ as wide as P⁴ rather than having P⁴ wider than M¹.

Etymology.—Latin, *-ensis*, suffix meaning from; allusion to Pratt Quarry.

Description.—The only known P₄ of *C. prattensis* is in the holotype. It is simple in occlusal mor-

phology, consisting of only four cusps with no accessory cusps. The crown-height index of the specimen (LEHP/TP) is 0.53, intermediate among species of *Cupidinimus* (Barnosky, 1986a:fig. 12). The cusps of the metalophid (protostylid, metaconid) are nearly equal in size and essentially round in outline. The hypolophid cusps (hypoconid, entoconid) are also equal in size but are oval in outline, the long axis being transversely oriented. The two lophi fuse at the center of the tooth.

The upper premolar on the only maxillary specimen (UNSM 101502) has a transverse width equal to that of M¹. P⁴ is longer (anteroposteriorly) than wide in nearly all specimens. The protoloph is made of a single round to oval protocone. None of the specimens of P⁴ have any accessory cusps on the protocone. The metaloph of P⁴ is made of three aligned cusps as is typical for the genus. The fusion of the lophi is central.

The occlusal morphology of the molars, again, is typical of the genus, consisting of two rows of three cusps. On the lower molars, the anterior cingulum originates at the protoconid and continues buccally to the protostylid. The anterior cingulum on the upper molars originates at the paracone, passes anterior to the protocone, and ends lingually at the protostyle. The crown height index for the lower molars (LEH/T) averages 0.44, higher than in *C. madisonensis* and *C. lindsayi*, but lower than all the other species measured by Barnosky (1986a:fig. 10). The upper molars have a crown height index (TOTH/T) that averages 0.64, lower crowned than all the species measured by Barnosky (1986a:fig. 13). The index of the height of the enamel chevron (CHEV/T) on the upper molars of *C. prattensis* is also lower than other species previously measured (Barnosky, 1986a:fig. 11).

Discussion.—*Cupidinimus prattensis* has relatively low-crowned cheek teeth, exceeding the crown height of only a few species either not measured or unknown to the last reviewer of the genus Barnosky (1986a): *C. boronensis*, *C. kleinfelderi*, and *C. smaragdinus* (Whistler, 1984; Korth, 1996b). The lack of accessory cusps on either the upper or lower premolars of *C. prattensis* is elsewhere consistent only with specimens of *C. lindsayi*, which is smaller and higher crowned than *C. prattensis* (Barnosky, 1986a).

Among its contemporary species of *Cupidinimus* (*C. quartus*, *C. tertius*, *C. cuyamensis*, and *C. avawatzensis*), *C. prattensis* has lower-crowned cheek teeth. It also lacks the accessory cusps on P⁴ or P₄ of these species. *Cupidinimus prattensis* is also smaller than *C. quartus* and *C. avawatzensis*. The unnamed species of *Cupidinimus* from the Clarendonian Mission fauna of South Dakota is smaller than *C. prattensis* and the figured P₄ appears to have an anterostylid (Green, 1971:text-fig. 2D).

As noted by Barnosky (1986a), the species of *Cupidinimus* from the Great Plains typically have lower-crowned cheek teeth than those from the Rocky Mountains and farther west. *Cupidinimus prattensis* is clearly part of this more eastern radiation of *Cupidinimus*. The remainder of the species in this eastern radiation (*C. nebraskensis*, *C. kleinfelderi*, and *C. smaragdinus*) are also characterized by commonly having accessory cusps on the premolars, especially P₄ (Storer, 1975; Korth, 1979, 1996b; Barnosky, 1986a). *Cupidinimus prattensis* differs from these species in this regard, lacking accessory cusps on either upper or lower premolars. *Cupidinimus prattensis* is similar in size and occurrence of accessory cusps on the premolars to the Barstovian *C. whitlocki* but differs from the latter in having slightly lower-crowned cheek teeth and having P⁴ longer than it is wide. *Cupidinimus whitlocki* is diagnosed as having a shortened upper premolar (Barnosky, 1986a).

The recognition of *Cupidinimus prattensis* increases the number of Clarendonian species of this genus to five (see Korth, 1994:186). This is a decrease from the nine Barstovian species, and part of the trend toward the diminishing numbers of species of this genus into the Hemphillian, where only a single species is recognized (Baskin, 1979).

?Subfamily Harrymyinae Wahlert, 1991

Lignimus Storer, 1970*Lignimus* sp.

(Fig. 7B, C, 8D)

Referred Specimens.—UNSM 101531, isolated M₁ or M₂; UNSM 101516, 101533, isolated M¹ or M²; and UNSM 101532, partial edentulous mandible.

Measurements.—Lower molar (UNSM 101531): a-p, 1.22 mm; tra, 1.32 mm; trp, 1.35 mm. Upper molars: UNSM 101516, a-p, 1.19 mm; tra, 1.43 mm; trp, 1.39 mm; UNSM 101533, a-p, 1.26 mm; tra, 1.75 mm; trp, 1.71 mm.

Description.—The cheek teeth are nearly identical in morphology to those of *Lignimus montis* and *L. austridakotensis* except in size. The mandible referred to *Lignimus* is robust for a heteromyid. The diastema is shallow and long. The masseteric scar has a strong ventral ridge that extends to a point just anterior to the roots of P₄, near the center of the mandible. At its anterior end it curves posteriorly. There is a very faint ridge marking the dorsal margin of the masseteric fossa that disappears below the alveolus for M₁. The mental foramen is small and directly anterior to the end of the masseteric ridge.

Discussion.—The specimens referred here to *Lignimus* are intermediate in size between *L. montis* and *L. austridakotensis* from the Great Plains (Storer, 1975; Korth, 1996b). The cheek teeth are not transversely elongated as in *L. transversus* from Wyoming (Barnosky, 1986b).

The mandible of *Lignimus* has never before been described. The allocation of the Pratt Quarry specimen to *Lignimus*, even though it lacks cheek teeth, is based on its comparable size with the cheek teeth identified as *Lignimus* and a lack of any other geomyoid in the fauna to which it could be allocated. The most intriguing character of the mandible is the masseteric scar. It is not typical of heteromyids with a small shelf that extends anterior to the tooth row, but is nearly identical to the masseteric scar on the mandible of the harrymyine *Harrymys irvini* (Wahlert, 1991:fig. 1). This similarity of the mandible reinforces the suggestion that *Lignimus* belongs in the Harrymyinae rather than any other group of geomyoid.

Lignimus is one of several species present at Pratt Quarry that is known elsewhere only from much earlier horizons (early to middle Barstovian) and thus these specimens might simply be reworked from the lower horizons present at Pratt Quarry. Once again, this is not likely because *Lignimus* specimens are known from the fossiliferous horizon 10 m above the basal channel and are not conspecific with any of the named species of the genus from the Barstovian.

Family ?Geomyidae Bonaparte, 1845

Phelosacomys Korth and Reynolds, 1994*Phelosacomys hibbardi* (Storer, 1973)

(Fig. 9, Table 8)

Lignimus hibbardi Storer, 1973.

Parapliosacomys hibbardi (Storer) Korth, 1987.

Phelosacomys hibbardi (Storer) Korth and Reynolds, 1994.

Referred Specimens.—UNSM 101561, 101773, P₄; UNSM 101577, isolated dP₄; UNSM 101562, 101570, isolated P^s; UNSM 101563–101569, 101571, 101574–101576, isolated molars; UNSM 101572, isolated upper incisor.

Description.—The dP₄ referred to *P. hibbardi* is low crowned and the roots are splayed. The tooth is much longer than any P₄ referred to the species. The hypolophid is made of four cusps that fuse together to form a wide loph. The largest cusps recognizable on the hypolophid are the hypoconid and entoconid, the former being the largest. A small hypoconulid is present posterior to the junction of the two main cusps. Buccal to the hypoconid is a small hypostylid. Anterior to the entoconid is a deep valley that separates the entoconid from the large, round metaconid. The remainder of the tooth

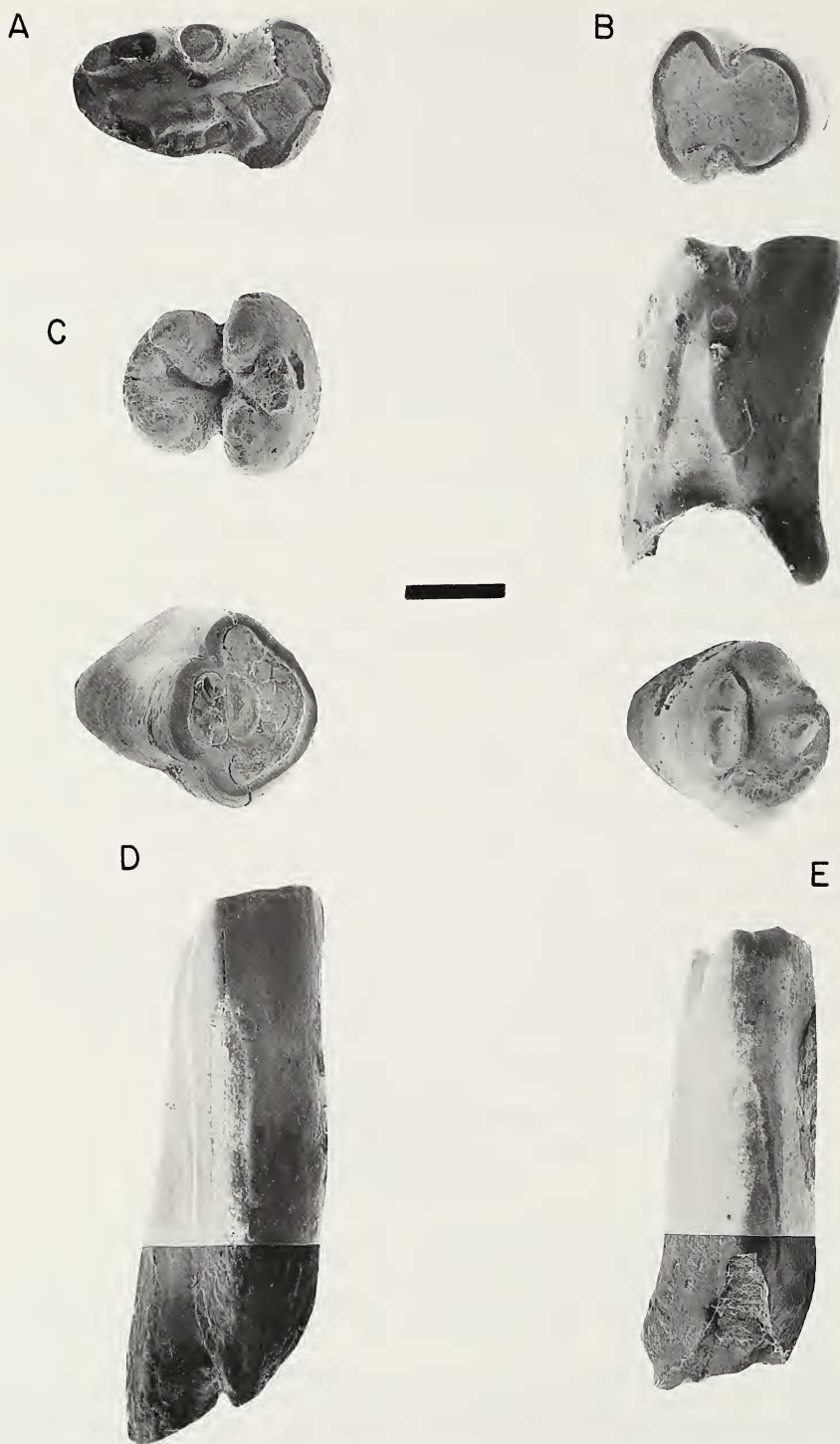


Fig. 9.—Scanning electron micrographs of cheek teeth of *Phelosacomys hibbari* from Pratt Quarry. A, left dP_4 , UNSM 101577. B, left P_4 (occlusal view above, lingual view below), UNSM 101773. C,

is surrounded by a series of seven small cusps that run along the buccal and anterior sides of the tooth and on the lingual side anterior to the metaconid. A small triangular cusp is located just anterior to the hypoconid in the center of the tooth.

Of the two P_{4s} represented from Pratt Quarry, one is unerupted (UNSM 101561) and the other is relatively well worn (UNSM 10173). On the unerupted tooth all cusps are visible. The metaconid and protostylid are nearly equal in size. There are two small anterostylids present, the lingual one is attached to the metaconid. Together these four cusps form an anteriorly convex lophid, isolating a central basin. The hypolophid is straight and made of two major cusps (entoconid, hypoconid) and a smaller, central hypoconulid. On the worn tooth the cusps have been lost on the occlusal surface and only a small enamel lake is present near the center of the tooth. On the sides of the unworn specimen there is a distinct dentine tract. The ratio of the dentine tract height (measured on the buccal side) to the posterior width of the tooth is 1.41. There are no roots evident on the worn P_4 .

As with the lower premolars, of the two P^4 s referred here to *P. hibbardi*, one is essentially unworn (UNSM 101570) and the other is well worn (UNSM 101562). On the unworn specimen there are three cusps of the metaloph that form a posteriorly convex arc (metacone, hypocone, hypostyle). The protoloph is narrower (buccolingually) than the metaloph and straight. It is made of two cusps, a larger protocone and a smaller, lingual protostyle. The lophs unite lingually. On the worn tooth the cusps are no longer distinguishable. The metaloph is still a wider curved loph and the protoloph a straight, shorter loph. The lophs, as in the unworn specimen, unite lingually. On the worn P^4 , the dentine tracts extend well up the sides of the tooth. The dentine tract height/transverse width ratio of this tooth is 75%. Below the base of the enamel there are the beginnings of roots forming on the worn P^4 .

The molars are hypsodont and the occlusal pattern of cusps is worn away on all specimens available, indicating that the cusps are lost at an early stage of wear. On the sides of the teeth there are dentine tracts. The ratio of the height of these dentine tracts to the transverse width of the teeth is 67–89% (mean = 79%). None of the available permanent teeth show any signs of having roots at any time, regardless of the amount of wear.

Discussion.—The small geomyid specimens from Pratt Quarry are clearly referable to *Phelosaccomys hibbardi* originally known from the Clarendonian of Kansas as diagnosed by Storer (1973). The only difference in the morphology of P_4 from Pratt Quarry is the presence of two anterostylids rather than three. The dentine tract on the sides of P_4 are also slightly higher in the Nebraska specimens than on those from Kansas. However, these differences are quite minor and are well within any range of variation of a single species.

The upper premolar of *P. hibbardi* has never before been identified. It is quite similar in occlusal morphology to that of *P. shotwelli* from the Clarendonian of California (Korth and Reynolds, 1994). Both *P. hibbardi* and *P. shotwelli* have anteroposteriorly compressed protolophs that form a straight line unlike that of older species where the protocone is more oval in shape (Korth, 1979). *Phelosaccomys hibbardi* and the Pratt Quarry specimens differ from *P. shotwelli* in having less well-developed dentine tracts on the cheek teeth, being larger, and having a P_4 that is longer than wide.

The dP_4 of *Phelosaccomys* has never been described previously. This tooth differs from those of heteromyids in having a reduced protoconid and numerous cusps that line the buccal and anterior sides of the tooth. This type of deciduous lower premolar is more typical of geomyids (Akersten, 1973). Lindsay (1972:fig. 34b) figured the dP_4 of the primitive geomyid *Mojavemys*. This tooth is very similar to dP_4 of *P. hibbardi*. The similarity of the deciduous premolars of these

←

right P_4 (unworn), UNSM 101561. D, left P^4 (occlusal view above, lingual view below), UNSM 101562. E, right P^4 (unworn: occlusal view above, buccal view below), UNSM 101570. Bar scale = 1 mm.

Table 8.—Dental measurements of *Phelosacomys hibbardi* from Pratt Quarry. Abbreviations as in Table 1. Additional abbreviation: *ht/tr*, crown height index (ratio of height of dentine tract to transverse width of tooth). Measurements in mm.

UNSM No.	dP ⁴		P ⁴			M ₁ or M ₂			P ⁴			M ¹ or M ²				
	a-p	tra	tp	tra	ht/tr	a-p	tr	ht/tr	a-p	tra	tp	ht/tr	a-p	tra	ht/tr	
101577	2.53	1.25	1.51													
101561				1.81	1.47	1.83										
101564							1.28	2.00	0.67							
101565							1.20	1.93	1.00							
101566							1.27	2.08	0.86							
101773				1.87	1.32	1.67			1.41							
101562										1.54	1.04	1.90	0.75			
101563																
101567													1.29	2.11		
101568													1.19	1.83	0.89	
101569													1.23	1.84		
101570										1.34	1.06	1.84		1.75	0.79	
101571													1.11	1.89		

taxa make them more likely geomyids than heteromyids, although their systematic position within the Geomyidae is not certain.

Family Cricetidae Rocheburne, 1883

Subfamily Peromyscinae Hershkovitz, 1966

Tregomys Wilson, 1968

Tregomys shotwelli Wilson, 1968

(Fig. 10A)

Gnomomys saltus Wilson, 1968.

Referred Specimen.—UNSM 101534, isolated right M_1 .

Measurements.—a-p, 1.39 mm; tra, 0.71 mm; trp, 0.90 mm.

Discussion.—The isolated M_1 referred to *Tregomys shotwelli* is nearly identical to M_1 of the holotype from Trego County, Kansas (Wilson, 1968). It is separable from all of the other cricetids from Pratt Quarry in being smaller (except *Copemys pisinnus*), having a central, symmetrical anteroconid (asymmetrical in other species), and lacking the complete alternation of cusps present in *Antecalomys phthanus* (described below). Voorhies (1990b) synonymized *Gnomomys saltus* with *T. shotwelli*. This synonymy is followed here.

Copemys Wood, 1936

Copemys pisinnus Wilson, 1968

(Fig. 10C, D, 11A; Table 9)

Referred Specimens.—UNSM 101535, left mandible with M_1 – M_3 ; UNSM 101536, right mandible with M_1 – M_3 ; and UNSM 101537, right maxilla with M^2 .

Discussion.—The Pratt Quarry specimens referred to *Copemys pisinnus* are inseparable from the topotypic material from Kansas in size and morphology (Wilson, 1968). The molars are simple, lacking mesolophids and other accessory cuspules and lophs. However, these specimens are also very similar to specimens of *C. dentalis* from the Clarendonian of Nevada and Oregon (Hall, 1930; Clark et al., 1964; Shotwell, 1967b). The holotype of *C. dentalis* is slightly larger than specimens of *C. pisinnus* from Kansas and Pratt Quarry (Clark et al., 1964:table 4; Wilson, 1968:table 18; Table 9, this paper), but all of these specimens are within the range of size of a large sample of *C. dentalis* from Oregon (Shotwell, 1967b:table I). The low frequency of accessory lophs and styles on the Oregon material is also compatible with the described material of both *C. pisinnus* and *C. dentalis*.

It is very likely that *C. pisinnus* is a junior synonym of *C. dentalis*. However, no formal synonymy will be proposed here because the type and topotypic material of *C. dentalis* were not available for this study. Direct comparison with the type material of *C. dentalis* is necessary before a definite synonymy can be proposed.

The *Copemys pisinnus* material is distinctly smaller than any of the other *Copemys* species present at Pratt Quarry (described below). Although this material is similar in size to the isolated M_1 referred above to *Tregomys shotwelli*, it differs from the latter in having the *Copemys* morphology of M_1 —asymmetrical anteroconid, and protoconid and metaconid not directly transversely aligned. In *T. shotwelli* the anteroconid is central and symmetrical, and the protoconid and metaconid are directly buccolingually aligned with no hint of alternation.

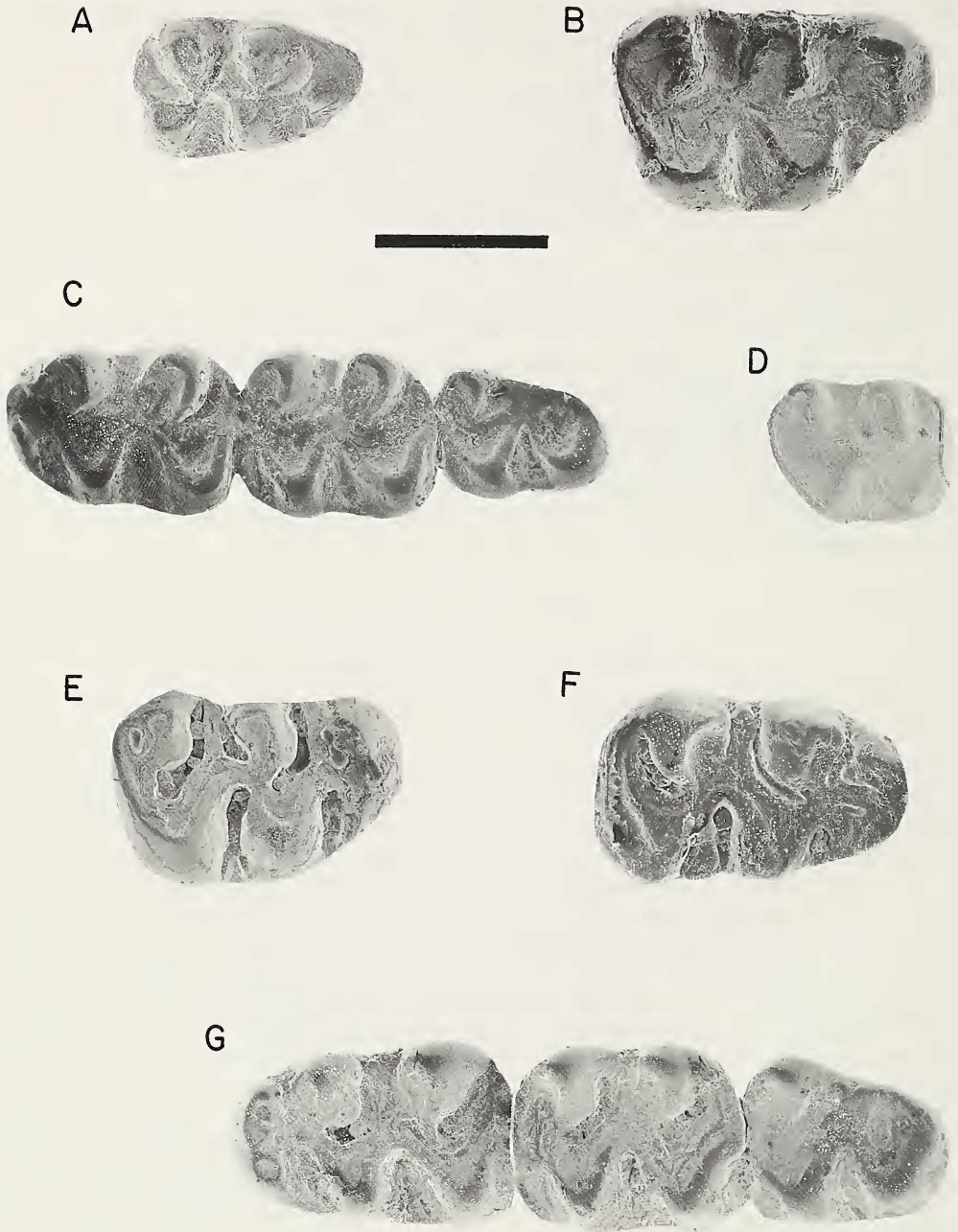


Fig. 10.—Scanning electron micrographs of cheek teeth of *Copemys* and *Tregomys* from Pratt Quarry. A, *Tregomys shotwelli*, right M_1 , UNSM 101534. B, *Copemys* sp., right M^1 , UNSM 101560. C, D, *Copemys pisinnus*. C, left M_1 – M_3 , UNSM 101535. D, right M^2 , UNSM 101537. E–G, *Copemys mariae*. E, right M^1 , UNSM 101593. F, right M_1 , UNSM 101541. G, left M_1 – M_3 , UNSM 101538. Bar scale = 1 mm.

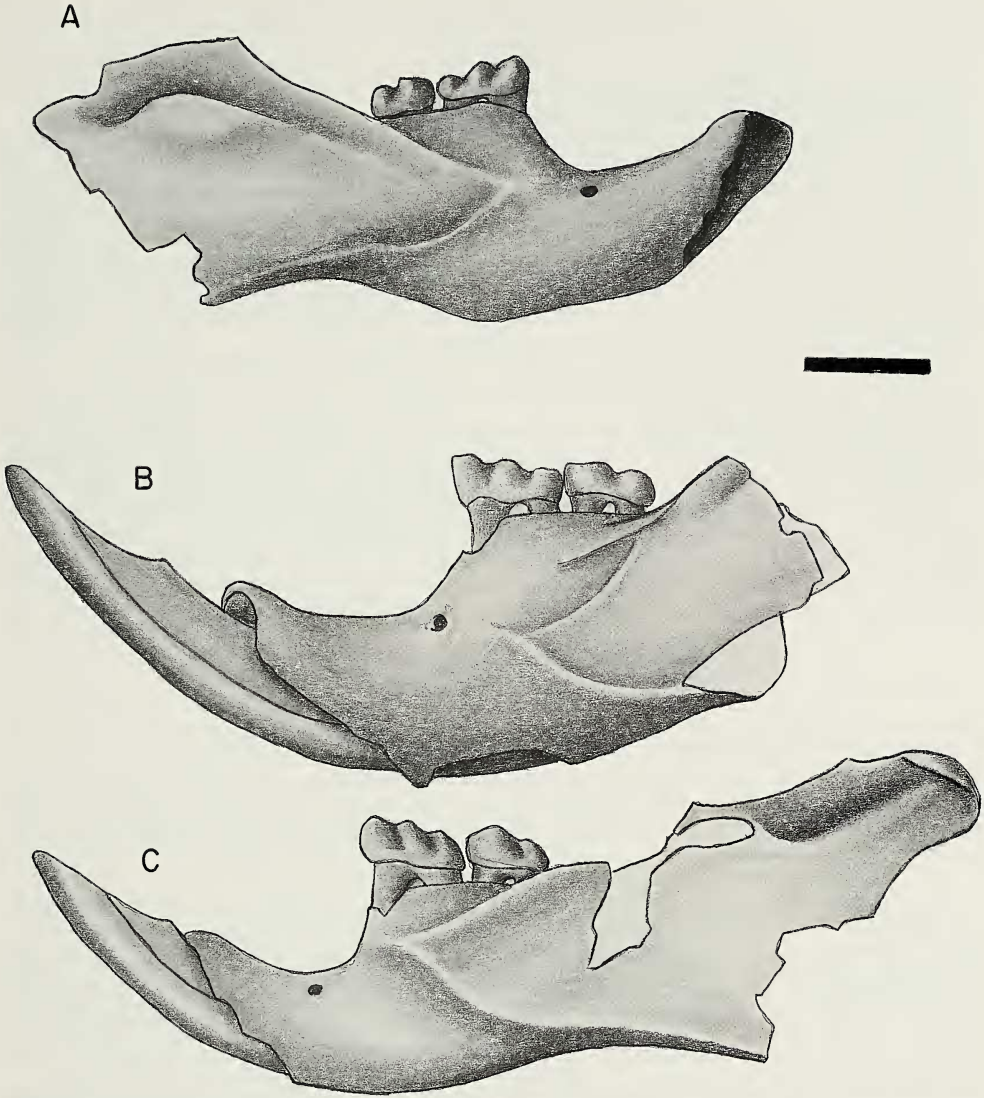


Fig. 11.—Mandibles of cricetid rodents from Pratt Quarry. All lateral views. A, *Copemys pisinnus*, UNSM 101536. B, *Copemys mariae*, UNSM 101539. C, *Antecalomys phthanus*, UNSM 101552. Bar scale = 2 mm.

Table 9.—Dental measurements of *Copemys pisinnus* from Pratt Quarry. Abbreviations as in Table 1. Measurements in mm.

UNSM No.	M ₁			M ₂			M ₃			M ₁ -M ₃	M ²		
	a-p	tra	trp	a-p	tra	trp	a-p	tra	trp		a-p	tra	trp
101535	1.31	0.86	0.99	1.12	0.99	0.96	0.98	0.76	0.70	3.49			
101536	1.48	0.85	1.00	1.19	0.92	0.94							
101537											1.00	0.84	0.84

Copemys sp.

(Fig. 10B)

Referred Specimen.—UNSM 101560, isolated right M¹.*Measurements*.—a-p, 2.00 mm; tra, 125 mm; trp, 127 mm.

Description and Discussion.—UNSM 101560 is considerably larger than any of the other cricetids from Pratt Quarry. The anterocone is weakly doubled, similar to the condition in the Barstovian to Clarendonian *Copemys russelli* (James, 1963; Lindsay, 1972). This tooth differs from *C. russelli* in being larger, lacking a paralophule and mesoloph, and having the protocone attached to the paracone by the protolophule II only. Besides its larger size, UNSM 101560 is distinct from all of the other cricetids from Pratt Quarry. It differs from *C. mariae* by lacking a mesoloph and other accessory lophids; from *Tregomys shoiwelli* and *C. pisinnus* by being over 50% larger; and from *Antecalomys phthanus* (described below) in having cusps more directly buccolingually aligned (not alternating) and lacking the accessory root and shallow anterior groove on the anterocone.

In size, UNSM 101560 is closest to the Clarendonian *Copemys esmeraldensis* (Clark et al., 1964: 53). It differs from upper molars of *C. esmeraldensis* in lacking a paralophule and mesoloph and being relatively narrower (buccolingually).

Storer (1975) reported a large sample of *Copemys kelloggae canadensis* (= *C. niobrarenensis*, Voorhies, 1990b) from the Barstovian of Saskatchewan that had a wide range of size and morphology which would include UNSM 101560. However, this sample appears to represent more than a single species because of the high coefficients of variation of the measurements (greater than 10) and extremely different morphologies present. A sample of probable topotypic specimens of *C. niobrarenensis* from Nebraska are clearly smaller than UNSM 101560 (Voorhies, 1990b:table A-10). The Canadian sample is also characterized by a very high percentage of long mesolophs, paralophules, and accessory cuspsules on M¹, unlike the specimen from Pratt Quarry.

Copemys mariae Baskin and Korth, 1996

(Fig. 10E–G, 11B; Table 10)

Copemys lindsayi Dalquest et al., 1996 (not *C. lindsayi* Sutton and Korth, 1995).

Referred Specimens.—UNSM 101538, left mandible with incisor and M₁–M₃; UNSM 101539, mandible with left M₁–M₂; UNSM 101540, mandible with right M₁–M₂; UNSM 101541, 101791, isolated M₁; UNSM 101792, right M₂; UNSM 101542, fragmentary mandible with left M₂; and UNSM 101593, right M¹.

Amended Diagnosis.—Differs from all species of *Copemys* except *C. esmeraldensis* and *C. barstowensis* in having well-developed mesolophs (-ids) and other accessory lophids on molars, complex anterocones (-ids) on first molars (often doubled) wearing to a broad (buccolingually) anterior loph, and having a mandible with a symphyseal eminence (chin process); differs from *C. esmeraldensis* and *C. barstowensis* in being smaller; a minute accessory root is variably present on M¹.

Description.—The mandible is more robust than other species of *Copemys* except *C. esmeraldensis* (Clark et al., 1964:fig. 9F). Along the ventral margin of the mandible, a small piece of bone has been broken away at the ventral end of the symphysis on all specimens, implying that there was a small eminence there (= "chin process"), similar to the morphology of *C. esmeraldensis*. The masseteric scar extends anteriorly to below the anterior root of M₁. The anterior end of the masseteric scar forms a V-shape. The dorsal ridge of the masseteric fossa is not coincident with the anterior margin of the ascending ramus for its anterior 2 mm. The ascending ramus arises level with M₃. There is a deep valley separating the ascending ramus from the tooth row. The mental foramen is high on the mandible at the posterior end of the diastema. The diastema is fairly deep and steeper on its posterior slope below P₄ than along its anterior slope.

The first lower molar is the largest of the tooth row. The anteroconid is broad and complex, often consisting of two or more cuspsules. It wears to a broad loph in specimens of older individuals. A loph runs from the anteroconid around the anterobuccal corner of the tooth, ending just anterior to the protoconid. The metalophid cusps unite anteriorly (metalophulid I) and fuse with the anteroconid near the center. The buccal cusps (protoconid, hypoconid) are crescentic, and the lingual cusps (metaconid, entoconid) are anteroposteriorly compressed. The mesolophid is always long, reaching the lingual margin of the tooth. On the buccal side of the tooth there is usually either a small ectostylid

Table 10.—Dental measurements of *Copemys mariae*. Abbreviations as in Table 1. Measurements in mm.

UNSM No.	M ₁			M ₂			M ₃			M ₁ -M ₃	M ²		
	a-p	tra	trp	a-p	tra	trp	a-p	tra	trp		a-p	tra	trp
101538	1.69	0.95	1.12	1.30	1.11	1.08	1.24	0.98	0.75	4.24			
101539	1.74	1.04	1.15	1.44	1.21	1.18							
101540	1.77	1.00	1.14	1.46	1.19	1.16							
101541	1.74	1.19	1.22										
101542				1.33	1.07	0.97							
101791	1.81	0.99	1.12										
101792				1.52	1.22	1.16							
101593											1.79	1.11	1.14

between the protoconid and hypoconid, or a distinct buccal mesolophid. The entoconid fuses with the anterior arm of the hypoconid. The posterior cingulum extends the entire width of the tooth. Dalquest et al. (1996) reported the variable occurrence of a small accessory root on topotypic M₁'s from Oklahoma. There is no indication of these accessory roots on the Pratt Quarry material.

The second lower molar is similar to M₁, lacking only the anteroconid. The metaconid is positioned along the anterior margin of the tooth, from which runs the buccal loph along the anterobuccal corner of the tooth. The mesolophid is long, often ending in a mesostylid. Commonly, there is an ectostylid between the buccal cusps. A distinct hypoconulid is preserved as a widening of the posterior cingulum, just posterior and lingual to the hypoconid.

The last lower molar is the smallest of the lower cheek teeth. Anteriorly, it is similar to M₂. The mesolophid is long and fuses with the posterior cingulum at its lingual end. The hypoconid is reduced and the entoconid is completely lacking. There is no indication of an ectostylid.

M¹ has a complex, broad anterocone. As in M₁, it consists of at least two minute cuspules. There is also a distinct paralophule between the anterocone and paracone. The lingual cusps are crescentic (protocone, hypocone) and the buccal cusps are round but anteroposteriorly compressed. The paracone joins the posterior arm of the protocone. The protocone joins the anterocone near its center by way of an anteroposteriorly directed loph. The mesoloph reaches the buccal margin of the tooth. The metacone joins the posterior cingulum near its center. There is a minute entostyle along the lingual border of the tooth between the lingual cusps. No other upper molars have been recovered.

Discussion.—*Copemys mariae* is based on several isolated cheek teeth from the middle to late Clarendonian of Oklahoma (originally called *C. lindsayi*; Dalquest et al., 1996). The size and morphology of the cheek teeth described here from Pratt Quarry do not differ from the topotypical material, and thus are clearly referable to this species.

Copemys mariae is the largest of the cricetids from Pratt Quarry except for the isolated tooth referred above to *Copemys* sp. Among species of *Copemys*, *C. mariae* most closely resembles *C. barstowensis* and *C. esmeraldensis* from the Barstovian or Clarendonian west of the Rocky Mountains (Clark et al., 1964; Shotwell, 1967b; Lindsay, 1972). All three species are characterized by bulbous cusps on the cheek teeth, robust mandibles with a chin process, complex anterocones (-ids) on the first molars, and accessory lophs and cuspules on the molars. These three species, *C. esmeraldensis*, *C. barstowensis*, and *C. mariae*, appear to form a lineage within *Copemys*, distinct from all other species.

Repenning (1968) pointed out several characters of the mandible of arvicolines that separated them from other cricetids, all related to a change in the masseteric musculature that was more advantageous to the propalinal chewing motion of arvicolidids. These features were: 1) ascending ramus originates more anteriorly (blocking M₂ laterally) and is steeper; 2) the dorsal margin of the masseteric fossa is posterior to, rather than coincident with, the anterior margin of the ascending

ramus; 3) there is a ventral symphyseal eminence (chin process); 4) there is a deep valley between the tooth row and the ascending ramus; and 5) the ventral margin of the masseteric fossa is shelf-like.

Of these features, three are present in the mandibles of *C. mariae*. The dorsal margin of the masseteric fossa on specimens of *C. mariae* ultimately joins the anterior margin of the ascending ramus, but not along the anterior part below the cheek teeth. This arrangement is nearly identical to that in the early Hemphillian arvicoline *Goniodontomys disjunctus* (Repenning, 1968:fig. 8). The chin process on specimens of *C. esmeraldensis* and *C. mariae* are also part of the arvicoline mandibular construction that is not present in other species of *Copemys*. The third arvicoline feature of the mandible of *C. mariae* is the deep valley between the tooth row and the ascending ramus (temporal fossa).

Dentally, there is nothing about the *C. barstowensis*–*C. esmeraldensis*–*C. mariae* lineage that is particularly reminiscent of the earliest arvicolines. However, the shared characters of the mandible are suggestive of a possible relationship. It has been suggested that at least the earliest subfamily of arvicolids, the Prometheomyinae, was derived from a *Copemys*-like cricetid (Martin, 1975). A North American ancestor for the Prometheomyinae is also suggested by the fact that the earliest arvicolids anywhere are the early Hemphillian prometheomyines *MicrotoscOPTES* and *Goniodontomys* from North America (Repenning et al., 1990). The Clarendonian occurrence of both *C. mariae* and *C. esmeraldensis* from Nebraska and Oregon, respectively, is consistent with the earliest occurrence of arvicolids from the early Hemphillian of the same areas.

The ancestry of the earliest arvicolids (= microtines) is still not certain, but the shared mandibular morphologies of *C. mariae* with these early North American arvicolids supports the hypothesis of a North American origin, at least for the Prometheomyinae.

Subfamily Sigmodontinae Wagner, 1843

Antecalomys, new genus

Peromyscus Gloger, Shotwell, 1967b (in part).

?*Copemys* Jacobs, 1977.

?*Copemys* Korth, 1994.

Type Species.—*Antecalomys phthanus* n. sp.

Referred Species.—*Antecalomys valensis* (Shotwell, 1967b), and *A. vasquezi* (Jacobs, 1977).

Range.—Late Clarendonian of Nebraska, and Hemphillian of Oregon and Arizona.

Diagnosis.—Small sigmodontine, differs from all other sigmodontines in the following characteristics: more weakly divided anterocone of M^1 , anteroconid asymmetrical to weakly divided on M_1 , alternation of cusps incomplete on upper molars (paracone not directly connected to hypocone) but complete on lowers, accessory rootlet on M^1 but not on M_1 , and M^3/M_3 markedly reduced in size relative to second molars; differs from contemporary sigmodontine *Abelmoschomys* in lacking accessory lophs (including mesolophs and mesolophids) and styles on the molars, and having alternation of cusps complete on the lower molars (protoconid and entoconid directly connected).

Etymology.—Latin, *ante*, before; and *Calomys*, possibly related rodent.

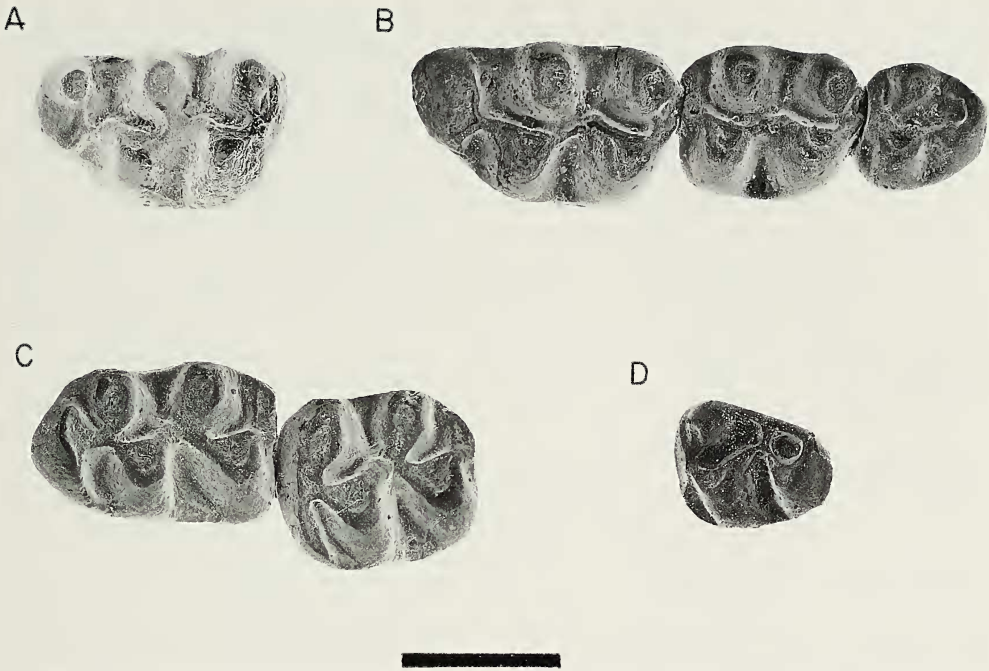


Fig. 12.—Scanning electron micrographs of cheek teeth of *Antecalomys phithanus*. A, holotype, left M^1 , UNSM 101543. B, left M^1 – M^3 , UNSM 101545. C, left M_1 – M_2 , UNSM 101552. D, left M_3 , UNSM 101553. Bar scale = 1 mm.

Discussion.—*Antecalomys* differs from contemporary cricetids based on the following dental characters: from *Copemys* Wood (1936) in having a split anterocone and accessory rootlet on M^1 ; from *Abelmoschomys* Baskin (1986) in its smaller size, less ovate first molars, the lack of accessory lophs (-ids) on the molars, and complete alternation of cusps on lower molars; and from *Tregomys* Wilson (1968) by the same characters as for *Copemys* as well as an asymmetrical anteroconid on M_1 (symmetrical in *Tregomys*). *Antecalomys* differs from other Tertiary sigmodontine rodents as follows: anteroconid on M_1 less well divided than in *Symmetrodontomys* and *Calomys* (*Bensonmomy*), anterocone on M^1 less well divided than in *Baiomys* and the former genera, accessory rootlet minute on M^1 but lacking on all M_1 s; cheek teeth much lower crowned than in *Prosigmodon* and *Sigmodon*, and alternation of cusps incomplete on upper molars (complete on other genera).

Antecalomys phithanus, **new species**

(Fig. 11C, 12; Table 11)

Type Specimen.—UNSM 101543, isolated left M^1 .

Referred Specimens.—UNSM 101544, 101546–101551, M^1 s; UNSM 101545, maxilla with M^1 – M^3 ; UNSM 101554, 101555, 101557, isolated M_1 s; UNSM 101556, isolated M_2 ; UNSM 101552, mandible with incisor and M_1 – M_2 ; UNSM 101553, 101558, mandibles with M_3 ; UNSM 101768, mandible with M_1 – M_3 ; and UNSM 101559, edentulous mandible.

Diagnosis.—Largest species of the genus; anterocone on M^1 less well divided than in other species.

Etymology.—Greek, *phthano*, come before or anticipate.

Description.— M^1 is the largest of the upper cheek teeth. The molars decrease in size from M^1 to M^3 . The anterocone on M^1 is transversely broad and buccally placed. A groove along the anterior slope divides the cusp. The depth of the groove is variable but is always present, although it never totally divides the anterocone into two separate cusps. The lingual cusps are crescentic (protocone, hypocone) and the buccal cusps are round to oval in shape (paracone, metacone). The anterior arm of the protocone joins the posterior wall of the anterocone lingual to its center. The paracone fuses with the posterior arm of the protocone just posterior to the posterobuccal corner of the protocone. Posterior to this junction, the central mure bends lingually before it joins the hypocone. The metacone joins the posterior arm of the hypocone just posterior to the posterobuccal corner of the hypocone. The posterior cingulum is extremely short. No specimens of M^1 have any accessory lophs or cusps. There is never a mesoloph. On the base of the tooth there is always a small to minute accessory root between the two main buccal roots above the paracone.

M^2 is similar to M^1 in the orientation of the cusps but lacks the anterocone. The anterior cingulum runs nearly the entire width of the tooth. The anterior arm of the protocone fuses with the anterior cingulum at its center. The paracone is only very weakly joined to the posterior arm of the protocone. On unworn specimens it appears to be completely isolated. All other features of M^2 are identical to M^1 .

M^3 is the smallest tooth. Only three cusps are recognizable: paracone, protocone, and hypocone. The hypocone is markedly reduced in size. The anterior cingulum is as in M^2 but anterior arms of both the paracone and protocone join the anterior cingulum near its center. The metacone is reduced to a posteriorly convex loph (posterior cingulum) that joins the hypocone lingually.

As with the upper molars, M_1 is the largest of the lower cheek teeth and the molars are progressively smaller from M_1 to M_3 . Again, as in the upper molars, none of the lower molars has a mesolophid or any other accessory lophs or cusps. The buccal cusps are crescentic (protoconid, hypoconid) and the lingual cusps are oval in shape (metaconid, entoconid). The anteroconid of M_1 is central but asymmetrical. A loph runs from the apex of the cusp down the buccal side and ends posteriorly along the buccal side of the tooth just anterior to the protoconid. The alternation of the cusps is complete. The posterior arm of the protoconid is continuous with the anterior arm of the entoconid. These two cusps are joined by a short, straight, obliquely oriented loph. The anterior arms of both the metaconid and protoconid join the anteroconid near its center. The metaconid is placed anterior to the protoconid. The anterior arm of the hypoconid joins the entoconid directly, just posterior to its junction with the protoconid. The posterior cingulum is short, not reaching the entoconid lingually.

The second lower molar is identical to M_1 except that it lacks the enlarged anteroconid. The metaconid is along the anterior border of the tooth and is continuous with an anterior cingulum that runs anterior to the protoconid, ending buccally before it reaches the protoconid. The arrangement of other cusps is as in M_1 .

The third lower molar is the smallest of the lower cheek teeth. The anterior cusps of M_3 are as in M_2 . The hypoconid is much reduced and the entoconid is totally lacking. The posterior arm of the protoconid extends to the lingual margin of the tooth and encloses a small enamel lake that is formed by the anterior arm of the hypoconid and posterior cingulum.

The mandible is slender. The masseteric scar extends anteriorly to below the anterior root of M_1 in a V-shape. The diastema is relatively short and shallow but has a steep posterior wall below M_1 . The mental foramen is high on the side of the mandible, nearly along the border of the diastema. The ascending ramus arises lateral to M_2 .

The lower incisor is narrow and convex anteriorly. The enamel surface is smooth.

Discussion.—*Antecalomys phthanus* is the most common cricetid from Pratt Quarry. It is intermediate in size between the other cricetids present, larger than *Copemys pisinnus* and *Tregomys shotwelli*, and smaller than *C. mariae* and *Copemys* sp. It also differs from *Copemys* and *Tregomys* as described above. *Antecalomys phthanus* is the oldest and most primitive species of the genus. Both *A. valensis* and *A. vasquezi* are Hemphillian in age and have a deeper groove on the anterior slope of the anterocone of M^1 .

The split anterocone and accessory root on M^1 of *Antecalomys* are diagnostic sigmodontine characters that allow for its allocation to this subfamily. The origin of the New World sigmodontines has been debated as to whether they were immigrant taxa from Eurasia or evolved in North America (see Baskin, 1986, for

review of arguments). The Clarendonian occurrence of *Antecalomys* and its similarity to species of *Copemys* support the arguments for a North American origin for the Sigmodontinae.

Family Zapodidae Coues, 1875

Megasminthus Klingener, 1966

Megasminthus species indeterminate

Referred Specimens.—UNSM 101770, right partial maxilla with M¹; UNSM 101771, right maxilla with alveoli for P⁴–M².

Description and Discussion.—The only tooth preserved is a badly abraded M¹ in UNSM 101770. The size of the tooth (a-p, 1.68 mm; tr, 1.40 mm) is within the range of M¹'s of *M. gladiofex* from the early Barstovian of South Dakota (Green, 1977:1008) and much smaller than those of *M. tiheni* from the middle and later Barstovian (Klingener, 1966:table 1; Storer, 1975:87; Green, 1977:1012; Korth, 1980:table 5). Much of the buccal side of the tooth has been removed due to abrasion, thus reducing the transverse measurement. In both species of *Megasminthus*, M¹ is wider than long. It appears that the only reason UNSM 101770 is longer than wide is due to this abrasion.

The occlusal morphology of UNSM 101770 is similar to other species of *Megasminthus* and distinct from species of sicistines in having much more robust, round cusps and a valley that separates the loph connecting the anterocone and protocone and the loph connecting the paracone to the mesocone and hypocone from one another. In contemporaneous sicistines (*Schaubeumys*, *Plesiosminthus*) these lophs are connected by the anterior half of the endoloph which runs from the mesocone to the protocone.

The specimens from Pratt Quarry are far too poorly preserved to be identified specifically. However, this is the latest occurrence of *Megasminthus*, being known only from the Barstovian. Again, as with the specimens of *Pseudotheridomys* and *Lignimus*, it is possible that these two zapodid specimens are reworked from the lower horizons at Pratt Quarry. But once again, these specimens are both from the fossiliferous horizon 10 m above the base of the channel, and thus less likely to have been reworked.

Order Lagomorpha Brandt, 1955

Family Ochotonidae Thomas, 1897

Hesperolagomys Clark, Dawson, and Wood, 1964

Hesperolagomys sp., cf. *H. galbreathi* Clark et al., 1964

Referred Specimen.—UNSM 101709, P².

Measurements.—a-p, 1.37 mm; tr, 2.55 mm.

Description and Discussion.—P² has never been described for any species of *Hesperolagomys*, but UNSM 101709 is similar in size to the topotypic material of *H. galbreathi* from Nevada (Clark et al., 1964). There are two very shallow reentrants on the lingual side of the tooth. The single anterior lobe is roughly circular in outline. Lingual to it is a cement-filled crescentic anterior reentrant. The buccal end of the tooth is broken but the maximum width of the tooth can still be measured. This tooth is similar to P² of *Russellagus* (Storer, 1975:fig. 83F), but is much smaller and the anterior lobe is not flattened anteriorly as in the specimen of *Russellagus*.

The occurrence of *Hesperolagomys* at Pratt Quarry is not unexpected because undescribed specimens of this ochotonid have been reported from other Clarendonian localities in northcentral Nebraska (Voorhies, 1990b).

Russellagus Storer, 1970

Russellagus sp.

(Fig. 13, Table 12)

Referred Specimens.—UNSM 101708, 101776, P³; UNSM 101706, 101707, lower molariform teeth.

Discussion.—The specimens referred here to *Russellagus* differ from those of the Barstovian type species, *R. vonhofi*, only in being slightly larger and lacking plications on the anterior wall of the talonid of lower molariform teeth. The Pratt Quarry material may well represent a distinct species of *Russellagus*, but it is too poorly known to name one at this time.

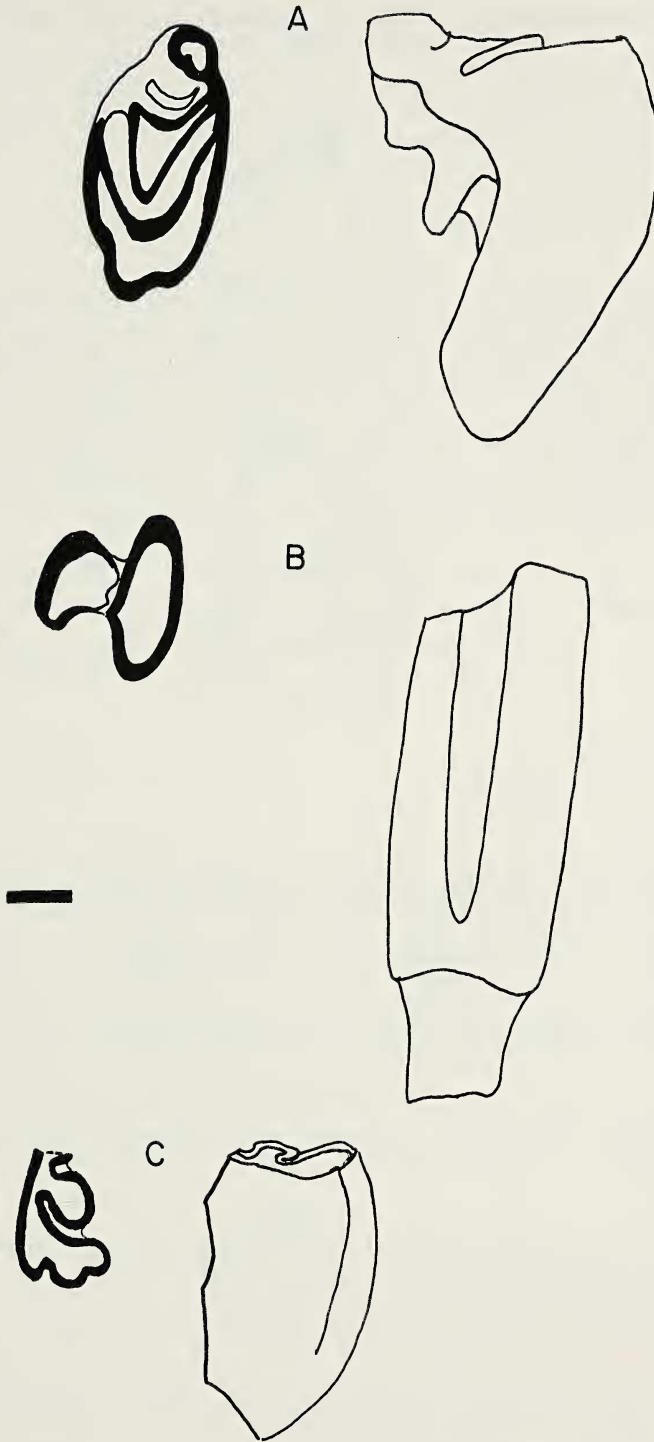


Fig. 13.—Cheek teeth of ochotonids from Pratt Quarry. A, B, *Russellagus* sp. A, left P³ (occlusal view left, anterior view right), UNSM 101708. B, right lower molariform tooth (occlusal view left, buccal view right), UNSM 101706. C, *Hesperolagomys* sp., cf. *H. galbreathi*, right P² (occlusal view left, posterior view right), UNSM 101709. Bar scale = 1 mm.

Table 12.—Dental measurements of *Russellagus* sp. from Pratt Quarry. Abbreviations as in Table 1. Measurements in mm.

UNSM No.	P ₃		Lower molar		
	a-p	tr	a-p	tra	trp
101708	2.05	4.13			
101706			2.35	2.87	1.80
101707			2.31	2.49	1.79

The specimens of *Russellagus*, as with some other species cited from this fauna, are last known from the late Barstovian, and there is no known record in the Clarendonian. This might imply that these specimens were reworked at Pratt Quarry from the Valentine Formation into which the deposit has cut. However, this is not likely the case for *Russellagus* because it has been recovered from all levels of the quarry including the diatomite layer at the top of the section. The lack of *Russellagus* from the Clarendonian in the Great Plains is more likely due to poor sampling for small mammals from rocks of this age.

Family Leporidae Fischer, 1817

Subfamily Archaeolaginae Dice, 1929

Hypolagus Dice, 1917

Hypolagus cf. *H. vetus* (Kellogg, 1910)
(Fig. 14A)

Lepus vetus Kellogg, 1910.

Hypolagus vetus (Kellogg), Dice, 1917.

Referred Specimen.—UNSM 101749, right P₃.

Measurement.—a-p, 3.48 mm.

Description and Discussion.—A single isolated P₃ from Pratt Quarry is much larger than any of the other specimens of leporids from this quarry. It is well within the range of size for *H. vetus* (White, 1987:table 2). The lingual edge of the tooth is broken away, so there is no way to determine whether or not there were any internal reentrant valleys. However, the two external reentrant valleys are of similar depth to those of *H. vetus* and lack any complex crenulations as in other species of *Hypolagus* (White, 1987, 1991).

The Barstovian *H. parviplicatus* is similar in size to *H. vetus* (Dawson, 1958; White, 1987; Voorhies, 1990b) but is characterized by shallower anterior and posterior reentrant valleys on P₃. The Pratt Quarry specimen has reentrant valleys equivalent to those of *H. vetus* and deeper than those of *H. parviplicatus*.

UNSM 101749 is the earliest record of *H. vetus* which is otherwise known only from the Hemphillian (Dawson, 1958; White, 1987). Specimens from the Barstovian of Saskatchewan originally referred to *Hypolagus* cf. *H. vetus* (Storer, 1975) were later allocated to *H. parviplicatus* (White, 1991).

Subfamily Leporinae Fischer, 1817

Alilepus Dice, 1931

Alilepus sp.

(Fig. 14B, C; Table 13)

Referred Specimens.—UNSM 101670, partial mandible with right P₃; UNSM 101772, 101784, P₃; UNSM 101671, 101672, 101783, lower molariform teeth; UNSM 101785, P₂; UNSM 101673, 101674, 101786–101788, 101790, 101793, upper molariform teeth.

Description.—The upper and lower molariform teeth referred here resemble those of *Hypolagus* as described elsewhere (Dawson, 1958). One of the P₃s assigned to *Alilepus* is of a very young individual, and the tooth has just come into occlusion (UNSM 101772). The occlusal pattern of the adult speci-

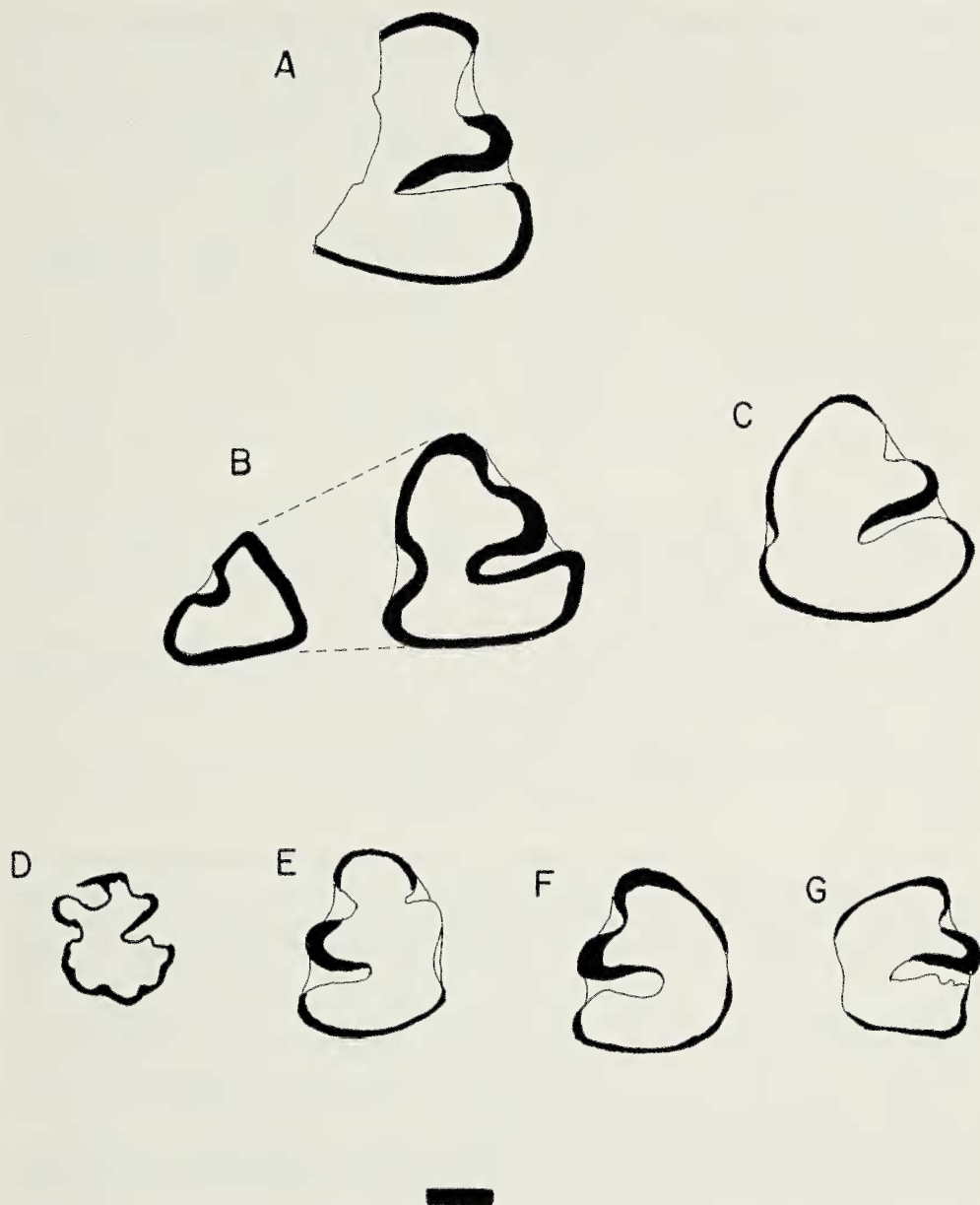


Fig. 14.—Lower third premolars of leporids from Pratt Quarry. A, *Hypolagus* sp., cf. *H. vetus*, right P₃, UNSM 101749. B, C, *Atilepus* sp. B, left P₃, UNSM 101772, occlusal surface (unworn) on left, base of crown on right. C, right P₃, UNSM 101670. D–G, *Pronotolagus whitei*. D, right P₃ (unworn), UNSM 101677. E, Holotype, left P₃, UNSM 101675. F, left P₃, UNSM 101676. G, right P₃, UNSM 101774. Bar scale = 1 mm.

Table 13.—Dental measurements of *Alilepus* sp. from Pratt Quarry. Abbreviations as in Table 1. Measurements in mm.

		n	M	OR	s	CV
P ₃	a-p	3	2.87	2.75–3.00	0.13	4.35
	tr	3	2.80	2.73–2.84	0.06	2.27
Lower molariform teeth						
	a-p	3	2.79	2.73–2.82	0.05	1.86
	tra	3	3.51	3.37–3.58	0.12	3.45
	trp	3	2.85	2.67–3.02	0.18	6.15
P ²	a-p	1	1.69			
	tr	1	3.00			
Upper molariform teeth						
	a-p	7	2.35	2.12–2.62	0.22	9.33
	tr	7	4.07	3.69–4.55	0.30	7.31

mens has two external reentrants. The anterior reentrant is shallow, extending 14% of the total width of the tooth; the posterior reentrant is deeper, extending 45% of the tooth. The posterior external reentrant is oriented just slightly posteriorly. There is a single internal reentrant even with the posterior external reentrant that is cement filled, and continues to the base of the crown. This internal reentrant is quite shallow, extending only 8% of the total width of the tooth.

The nearly unworn P₃ has a simple occlusal pattern with only a single, shallow external reentrant. However, the tooth gradually becomes wider toward its base, and at about half its height, there are two external reentrants and a single internal reentrant. The pattern of the base of the crown of this tooth is nearly identical to that of the adult specimen.

The isolated P² referred to *Alilepus* is similar to that of other species of the genus (White, 1991). There is a main anterior reentrant just lingual to the center of the anterior margin of the tooth that is deep, and curves slightly buccally. Buccal to it is a much smaller reentrant. Both reentrants are cement filled.

Discussion.—The specimens referred here to *Alilepus* fit the diagnosis of the genus (White, 1991:69) by maintaining a distinct posterior internal reentrant along with the two external reentrants on P₃. The Pratt Quarry specimens differ from P₃s of all other species in having the length of the tooth subequal to the width (in all other species this tooth is relatively longer than wide), and having a posterior internal reentrant very shallow. In all other species the posterior internal reentrant of P₃ is nearly as deep as the posterior external reentrant and often closes off lingually to form a small enamel lake. The Pratt Quarry specimens of *Alilepus* are larger than those of *A. wilsoni*, but smaller than the other two North American species of the genus (White, 1991:table 3).

Among species of *Alilepus*, the Pratt Quarry species most closely resembles *A. hibbardi* from the late Clarendonian and possibly early Hemphillian. They differ from *A. hibbardi* in being smaller and having P₃ more square with a shallower posterior internal reentrant. White (1991:fig. 11I) figured an isolated P₃ from the late Clarendonian of California that is similar in the structure of P₃ to the Pratt Quarry specimens. He referred this specimen to *Pronotolagus* sp. The Pratt Quarry specimens are larger than this specimen, and more squared. It is questionable whether the California specimen should be referred to *Pronotolagus* because of its similarity to *Alilepus*. This was also noted by White (1991:81) in his description of the specimen.

The most unusual feature of the P₃s referred here to *Alilepus* is the apparent ontogenetic change from a simple occlusal pattern to a more complex one. The

Table 14.—Dental measurements of *Pronotolagus whitei*. Abbreviations as in Table 1. Measurements in mm.

		n	M	OR	s	CV
dP ₄	a-p	2	1.93	1.92–1.94		
	tra	2	1.90	1.76–2.04		
	trp	2	1.52	1.49–1.55		
P ₃	a-p	5	2.26	2.08–2.42	0.12	5.42
	tr	5	1.92	1.67–2.05	0.15	8.00
Lower molariform teeth						
	a-p	7	2.60	2.26–2.93	0.22	8.50
	tra	7	2.79	2.44–3.02	0.23	8.25
	trp	7	2.40	2.21–2.67	0.18	7.67
M ₃	a-p	3	1.65	1.50–1.87	0.19	11.67
	tra	3	1.68	1.46–1.86	0.20	12.05
	trp	3	1.11	1.05–1.19	0.07	6.50
dP ²	a-p	1	1.20			
	tr	1	1.98			
Upper molariform teeth						
	a-p	8	1.85	1.53–2.11	0.19	10.21
	tr	8	3.34	2.96–3.60	0.25	7.35

species of *Pronotolagus* from Pratt Quarry (described below) shows a very different sequence, from complex to more simplified.

Pronotolagus White, 1991

Pronotolagus whitei, new species

(Fig. 14D–G, Table 14)

Type Specimen.—UNSM 101675, isolated P₃.

Referred Specimens.—UNSM 101678, 101781, dP₄; UNSM 101676, 101677, 101679, P₃; UNSM 101680–101684, 101782, 101789, lower molariform teeth; UNSM 101685, 101778, 101780, M₃; UNSM 101694, dP²; UNSM 101686–101693, 101777, 101779, upper molariform teeth; UNSM 101695, I¹; UNSM 101696, 101705, partial humeri.

Diagnosis.—Near size of *P. apachensis*; differs from *P. apachensis* in having a deeper posterior external reentrant on P₃ (ranging from 50–62% of the width of tooth) and having the posterior reentrant inclined anteriorly rather than posteriorly.

Etymology.—Patronym for John White for his noted work on later Tertiary leporids.

Description.—The occlusal morphology of adult P₃s is similar to those of species of *Hypolagus*. There are two external reentrants. The anterior external reentrant is shallow, extending 17–20% of the width of the tooth and is widely open buccally. The posterior reentrant is deep, ranging from 56–62% of the width of the tooth and angled slightly anteriorly. The lingual margin is either straight or gently concave. The enamel on the lingual side of the tooth is very thin.

The unerupted or juvenile P₃s have two internal and two external reentrants. The external reentrants are similar to those of the adult specimens, but the anterior reentrant is slightly deeper than in the adult specimens (slightly higher than 20% of the width of the tooth) and the posterior external reentrant is slightly shallower than the adult specimens (about 50% of the width). The internal reentrants are shallow, not exceeding 15% of the total width of the tooth. The grooves on the lingual side of the tooth marking the internal reentrants diminish toward the bases of these teeth and are gone at the base of the teeth. The anterior internal reentrant has a narrow lingual opening, whereas the posterior internal reentrant has a broad lingual opening.

The lower molariform teeth (P₄–M₃) resemble those of *Hypolagus* and other leporids. Similarly, the upper molariform teeth (P⁴–M³) resemble those of species of *Hypolagus* as well. No specimens of P³

have been recovered from Pratt Quarry. The hypostriae of the upper molariform teeth, however, differ with wear. On some specimens, the walls of the hypostriae are smooth and others are highly crenulated. There are also specimens that show an intermediate morphology, where the walls of the hypostriae are smooth for about half of their extent, and then become crenulated.

Discussion.—The range of variation of the internal reentrant valleys on the P_3 s assigned here to *Pronotolagus whitei* is similar to the amount of variation described and figured for the type species of the genus, *P. apachensis* (White, 1991: fig. 11A). The only difference between the Pratt Quarry material and specimens of *P. apachensis* is the depth and orientation of the posterior reentrant valley on P_3 . In *P. apachensis* the posterior external reentrant ranges from 40–49% of the width of the tooth, and is deflected slightly posteriorly. On specimens of *P. whitei*, the posterior external reentrant ranges from 50–62% of the total width of the tooth, and is deflected slightly anteriorly.

It appears that the variation in the depth of the internal reentrant valleys on P_3 of *Pronotolagus* are due to the age of the individual. On specimens with unworn or little-worn teeth, the internal reentrants are the largest, and in older individuals they are lost. On the internal sides of the little-worn P_3 s available from Pratt Quarry, it is evident that the grooves on the internal side of the tooth marking the reentrants become shallower toward the base of the crown. It appears likely that this is also the case with *P. apachensis* which has the same type of variation of the internal reentrants on P_3 (White, 1991:fig. 11A).

The variation in the amount of crenulations in hypostriae of the upper molariform cheek teeth from Pratt Quarry is also consistent with upper cheek teeth referred to *P. apachensis* from its type locality (Wood, 1937). The consistency of the morphology of the upper cheek teeth along with the similarities in the morphology of P_3 make this species clearly referable to *Pronotolagus*.

The recognition of *Pronotolagus* in the late Clarendonian of the northern Great Plains is consistent with its early Hemphillian occurrence elsewhere in Nebraska (White, 1991). The P_3 s from the early Hemphillian LeMoyne Quarry of Nebraska referred to *P. apachensis* (White, 1991:fig. 11B) differ from the Pratt Quarry material in having deeper, more persistent anterior internal reentrants but are similar in having the posterior external reentrant tilted anteriorly rather than posteriorly. The specimens from the Hemphillian may well represent a distinct species of *Pronotolagus* more closely related to *P. whitei* than the type species from California.

CONCLUSIONS

The rodent and lagomorph fauna from Pratt Quarry, represented by 25 species and over 300 specimens, is more diverse than any other from the Clarendonian of the Great Plains (Appendix). Its diversity is even greater than that of any of the Clarendonian microfaunas known from west of the Rocky Mountains (Wilson, 1939; James, 1963; Clark et al., 1964; Shotwell, 1970). Previously, only 12 species of rodents and lagomorphs had been cited from all levels of the Clarendonian of Nebraska (Voorhies, 1990a) and only five had been described (Webb, 1969a). This greater diversity of small mammals gives a much more complete picture of the Clarendonian fauna from the Great Plains.

There are four taxa from the Pratt Quarry that are characteristic of Hemphillian or later faunas: the beaver *Dipoides*, sigmodontine cricetids, the archaeolagine rabbit *Hypolagus vetus*, and leporine rabbits. Of these, leporine rabbits and a single sigmodontine cricetid have been reported elsewhere in North America from

Clarendonian deposits (Baskin, 1986; White, 1991). These first occurrences suggest a latest Clarendonian age for the fauna that consists of otherwise typically Clarendonian rodents and lagomorphs. None of the taxa cited here as first occurrences are immigrants into North America, but rather are more likely to have evolved from earlier North American animals.

The Hemphillian of Nebraska and the Great Plains is well documented so the micromammalian fauna is well known (Hibbard, 1953, 1964; Schultz, 1990; Voorhies, 1990a). These faunas lack a number of taxa present at Pratt Quarry that are characteristic of Clarendonian or earlier ages. This indicates the last occurrence of these taxa: the sciurids *Protospermophilus* and *Petauristodon*, the beaver *Eucastor*, the geomyid *Phelosacomys*, the heteromyid *Mioheteromys*, the cricetids *Copemys* and *Tregomys*, and the ochotonid *Hesperolagomys*.

Along with the combination of first and last occurrences that indicates a late Clarendonian age for the fauna from Pratt Quarry is a change in the proportions of the rodent fauna that also reflects a time of transition between Clarendonian and Hemphillian ages. The Clarendonian rodent fauna, in terms of diversity of rodent families, is similar to Barstovian faunas in that there is a great diversity of heteromyids and relatively few species of cricetids. In Hemphillian faunas the number of heteromyid species drops drastically and the number of cricetids increases several times (Korth, 1994:table 1). The fauna from Pratt Quarry is clearly transitional in retaining some diversity in the heteromyids, but not as great as in the Barstovian faunas, and having an increase in the diversity of cricetids, although not as great as in Hemphillian faunas.

Four genera described here from Pratt Quarry have been reported previously only from the Barstovian or earlier. All four of these taxa—*Russellagus*, *Lignimus*, *Pseudotheridomys*, and *Megasmithus*—are represented by only a few isolated dental elements in the Pratt Quarry fauna. Of these, *Russellagus* is the best represented, specimens having been recovered from all levels of Pratt Quarry. It might be argued that the specimens representing these taxa are reworked from the lower horizons into which the channel at Pratt Quarry was cut.

While reworking is a possibility, there are several arguments against this suggestion. First, the record of micromammals from earlier Clarendonian horizons in northcentral Nebraska is negligible. There are no other microvertebrate faunas younger than Barstovian and older than Hemphillian in Nebraska (see Voorhies, 1990a), and there are only two other micromammal faunas in the entire Great Plains that are Clarendonian in age (Wilson, 1968; Green, 1971). The occurrence of these small mammals at Pratt Quarry might prove to be continuous if the record of rodents and lagomorphs from early and middle Clarendonian horizons in the Great Plains was better known.

The second argument against reworking is the levels of occurrence at the quarry itself. Both *Russellagus* and *Lignimus* are represented in at least two horizons, not just the basal channel where the obviously reworked bone chips can be found. The specimens of *Megasmithus* are from the fossiliferous level 10 m above the base of the channel, again making it less likely that these specimens were reworked. *Pseudotheridomys* is the only one of these taxa represented from the basal channel at Pratt Quarry only. However, in this case, no specimens of *Pseudotheridomys* have been reported from any quarry in the medial or later Barstovian Valentine Formation in Nebraska (Voorhies, 1990a). The closest geographic occurrence is a possible specimen of *Pseudotheridomys* reported from the medial Barstovian Bijou Hills fauna in South Dakota (Korth, 1996b).

In the case of both *Russellagus* and *Lignimus*, the specimens described above from Pratt Quarry are not assignable to any recognized Barstovian species. If these taxa were identical with the species described elsewhere, it would add support to the reworked hypothesis. However, both of these genera have species that are well represented in the Barstovian of the Great Plains (Storer, 1975; Voorhies, 1990b; Korth, 1996b) but the Pratt Quarry material is distinct from these described species.

Finally, the preservation of the specimens of these previously Barstovian-only taxa from Pratt Quarry does not differ from that of the rest of the fauna. All specimens from Pratt Quarry show some level of abrasion, simply attesting to the fluvial environment in which they were deposited.

Ultimately, it is possible that these four genera of rodents and lagomorphs are reworked from lower horizons at Pratt Quarry. However, it is equally likely, if not more likely, that they are truly a part of the fauna. If, indeed, they are correctly identified as belonging to the Pratt Quarry fauna, then they all represent last occurrences.

Webb (1969b) argued that there were proportionally fewer rodents and lagomorphs from the Clarendonian than from either the Barstovian or the Hemphillian. He believed that the low number of these small herbivores was a true representation of the Clarendonian fauna rather than an artificially reduced number due to factors such as collecting bias. However, with 25 species of rodents and lagomorphs recognized from Pratt Quarry, it appears that the low number of these small mammals previously reported from the Clarendonian was not a true representation of the complete fauna. Preliminary faunal lists presented by Voorhies (1990a) from early and middle Clarendonian localities in Nebraska also suggest that the small herbivore fauna throughout the Clarendonian was much more diverse than suggested by Webb (1969b).

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APPENDIX

Faunal list of rodents and lagomorphs from Pratt Quarry.

Rodentia

Mylagaulidae

Mylagaulus monodon

Sciuridae

Protospermophilus sp., cf. *P. quatalensis*

Ammospermophilus junturensis

Spermophilus (Otospermophilus) sp.

cf. *Petauristodon* sp.

cf. *Sciurion* sp.

Castoridae

Eucastor planus

Dipoides tanneri

Hystricops sp., cf. *H. venustus*

Eomyidae

?*Pseudotheridomys* sp.

Heteromyidae

Mioheteromys sp., cf. *M. agrarius*

Cupidinimus prattensis

Lignimus sp.

Geomyidae

Phelosacomys hibbardi

Cricetidae

Copemys pisinnus

C. mariae

Copemys sp.

Tregomys shotwelli

Antecalomys phithanus

Zapodidae

Megasminthus sp.

Lagomorpha

Ochotonidae

Hesperolagomys sp., cf. *H. galbreathi*

Russellagus sp.

Leporidae

Pronotolagus whitei

Hypolagus sp., cf. *H. vetus*

Alilepus sp.